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Memory Influences Visual Cognition across Multiple Functional
States of Interactive Cortical Dynamics

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ABSTRACT

Memory supports a wide range of abilities from categorical perception to goal-directed behavior, such as decision-making and episodic recognition. Memory activates fast and surprisingly accurately and even when information is ambiguous or impoverished (i.e., showing object constancy). This paper proposes the multiple-state interactive (MUSI) account of object cognition that attempts to explain how sensory stimulation activates memory across multiple functional states of neural dynamics, including automatic and strategic mental simulation mechanisms that can ground cognition in modal information processing. A key novel hypothesis of this account is ‘multiple-function regional activity’: The same neuronal population can contribute to multiple brain states, depending upon the dominant set of inputs at that time. In state 1, the initial fast bottom-up pass through posterior neocortex happens between 95 ms and ~250 ms, with knowledge supporting categorical perception by 120 ms. In state 2, starting around 150 to 230 ms, a sustained state of iterative activation of object-sensitive cortex involves bottom-up, recurrent, and feedback interactions with frontoparietal cortex. This supports higher cognitive functions (e.g., those associated with decision-making) even under ambiguous or impoverished conditions, phenomenological consciousness, and automatic mental simulation. In the latest state so far identified, state M, starting around 300 to 500 ms, large-scale cortical network interactions, including between multiple networks (e.g., control, salience, and especially default mode), further modulate posterior cortex. This supports elaborated cognition based on earlier processing, including episodic memory, strategic mental simulation, decision evaluation, creativity, and access consciousness. Convergent evidence is reviewed from cognitive neuroscience of object cognition, decision-making, memory, and mental imagery that support this account and define the brain regions and time course of these neural dynamics.

Key words:

visual perception; decision making; long-term memory; object cognition; event-related potential

Human memory is activated rapidly, within 1 s, to support a wide range of abilities from categorical perception to goal-directed behavior, such as decision-making and episodic recognition. Memory activation is not only fast but also surprisingly accurate and robust even when stimulus information is ambiguous or impoverished (i.e., showing object constancy, e.g., categorizing a dog regardless of viewing conditions). This paper proposes the multiple-state interactive (MUSI) account of visual object cognition that attempts to explain how sensory stimulation activates memory across multiple functional states of neural dynamics, including mental simulation mechanisms that ground cognition in modal information processing. These states build upon each other over time, thereby successively enabling increasingly more sophisticated cognitive abilities. The central idea of this account is that posterior cortical areas are activated at different times in stimulus processing during multiple “states” of cortical neural dynamics that perform distinct functions (Schendan & Ganis, 2012; Schendan & Kutas, 2007a; Schendan & Maher, 2009; Schendan & Stern, 2008). Certain neural processes characterize each state, distinguish between states, and determine the types of global functions for cognition that can happen in each. Key differences between states are in interactive cortical dynamics that can occur between the posterior areas and feedback, recurrent, reentrant and recursive computations, especially those involving frontoparietal regions. So far, three states have been proposed. Each state is associated with a major hypothesis about the types of cortical dynamics and their function in cognition. The MUSI account is based on convergent cognitive neuroscience studies of visual object perception, cognition and memory but can also explain the dynamics of cognition in general, including for other sensory modalities, though details would differ.

1 Overview of MUSI account

1.1 Brain state: Definition and relevance

A brain ‘state’ has been defined as synchronous neural firing reflected in the electrical activity of the brain (Brown, 2006). The MUSI account expands this to define a brain ‘state’ as large-scale global, neurophysiological activity that differs qualitatively in structure and function from other brain states. The particular brain structures involved in a state are part of each state’s definition. MUSI focuses on synchronous brain states revealed using event-related brain potentials (ERPs). However, whether this activity is synchronous or not may vary with the state and its function, as variations in spike rate instead of synchrony of V1 neurons is associated with perceptual organization, awareness and attention (Lamme, 2003; Lamme, Super, Landman, Roelfsema, & Spekreijse, 2000).

The idea of distinct brain states of neuronal activation helps advance cognitive neuroscience for several reasons. 1) Despite decades of discussion of brain states, theoretical accounts of them are scant (Brown, 2006, 2012). 2) States capture important observations from dynamic, large-scale neurophysiological responses that have not yet been articulated within theoretical neuroscience. 3) States are important for relating brain activity to the mind. The MUSI account describes processing times and functional properties that distinguish between some brain states, so methods with sufficient temporal resolution (e.g., ERPs) are necessary to study them; note, methods with poor temporal resolution (e.g., functional magnetic resonance imaging, fMRI) may reflect multiple temporally overlapping states, leading to erroneous interpretations of function. For example, different states are associated with different patterns of neural responses, which, if smeared across a time period, would yield a mixed and potentially misleading pattern. 4) Bayesian, adaptive resonance theory (ART), and other computational theories posit feedback processes are critical for cognition (Fazl, Grossberg, & Mingolla, 2009; Friston, 2010), and evidence suggests that different states of feedback have different functions (Lamme & Roelfsema, 2000).

1.2 Multiple-function regional activity: An overarching hypothesis

In its current form, the MUSI account describes three states for visual object perception and cognition, and ‘multiple-function regional activity’ is a key novel hypothesis: The same regional neuronal population can contribute to multiple brain states, depending upon the dominant set of inputs to the region at that time. Specifically, the 3 essential brain states hypothesized so far to support healthy human cognition include activity within a neuronal population (e.g., cortical area such as the fusiform face area, FFA) that contributes different functions in different states. These functions are determined by the inputs that dominate the neurophysiological response of the cortical region (e.g., FFA), such as bottom-up, recurrent, and feedback or top-down (David, Harrison, & Friston, 2005). The key point is that the neuronal population (or cortical area) is activated at different times in stimulus processing via different neuronal processes. Further, this multi-faceted activation pattern thereby results in different neural computations and thus different functional outputs and associated roles in cognition for different states. The MUSI account has focused on the structural level of a cerebral cortical area, which is a 2-3 mm thick region of gray matter composed of multiple neuronal layers (six for neocortex) that performs a function that is distinct from other such areas (e.g., area V4 is necessary for color perception, whereas area V5 is necessary for motion perception), and cortical areas are organized hierarchically from simpler to more complex processing in the feedforward processing direction with multiple, intertwined processing streams and extensive interareal and feedback processes (Felleman & Van Essen, 1991). The neurophysiological state can theoretically be defined from the cortical area down to the neuronal level, a more holistic goal for future work. Already, similar accounts have been proposed at the neuronal level in primary visual area V1, as in classical versus non-classical receptive fields of the same neuron (Lamme, 2003; Lamme & Roelfsema, 2000).

Neurally-realistic computational modelling of event-related electromagnetic potentials (David et al., 2005; David et al., 2006) supports the MUSI account and suggests the dynamics of a neurophysiological state from neuronal to cortical area levels of brain architecture. Specifically, a neural mass model of hierarchically arranged cortical areas has been developed with feedforward, feedback, and lateral connections (David et al., 2005). In line with state 1 in the MUSI account, when feedforward inputs are sufficiently strong, excitatory interneuron responses saturate, resulting in an inherently stable state. The evoked responses generated by the model resemble early evoked potentials, such as the face-specific N170 (David et al., 2006). In contrast, and in line with MUSI state 2, when feedback or lateral (or recurrent) connections are added to the model, cortical dynamics change. Neurophysiological potentials increase in duration and show damped oscillations when top-down inputs are relatively smaller, and responses resemble later endogenous potentials, such as the N400 or P300, indicating that re-entrant dynamics within cortical hierarchies underlie the late potentials. In contrast, when top-down inputs increase above a threshold, a phase-transition occurs and time-locked oscillatory dynamics dominate and stabilize and become maximal around 500 ms. Such late stable oscillatory dynamics may underlie state M in the MUSI account. Bilateral connections additionally cause zero-lag phase-locking among cortical areas. This is consistent with the MUSI idea that a state can involve multiple cortical areas, such as prefrontal and inferotemporal cortices.

In addition, when empirical data are used to estimate the parameters in this computational model and dynamic causal modeling of specific cortical areas is used, an increase in feedforward connectivity along the ventral visual pathway is associated with neurophysiological potentials resembling the face-specific N170 (David et al., 2006), consistent with MUSI state 1. Moreover, using a similar model with auditory oddball paradigm data, standards (e.g., frequent high tones)

and oddballs (e.g., rare low tones) differ for the first time when feedback processes begin to contribute during later neurophysiological potentials (i.e., state 2), specifically the mismatch negativity, but not during earlier potentials (i.e., state 1), such as the N100 (David et al., 2006); note, addition of lateral (recurrent) connections was not superior to feedback connections alone, indicating feedback connections are most important for the functional processes underlying later neurophysiological potentials. Further, learning-related changes in feedforward and feedback connections drive the development of later potentials (David et al., 2006), indicating that learning is related to feedback processing during the second state of cortical dynamics. This is consistent with the MUSI account of state 2.

1.3 MUSI states 1, 2 and M: Overview and main hypotheses

MUSI also aligns with the hierarchy of convergent and divergent cortical anatomy and convergence/ divergence zones (A. R. Damasio, 1989; Meyer & Damasio, 2009), which indicates that states typically occur in a particular sequential order (David et al., 2005). Processing in a previous state needs to start before processes in the next state that depend upon that state can start. States can overlap in time. In fact, source estimation suggests state 1 can continue throughout later states, presumably because the processes continue to be needed for later states (Schendan & Lucia, 2010).

The MUSI account was developed primarily to explain the cortical dynamics supporting tasks that emphasize ventral visual pathway processing, knowledge and memory, such as category decisions (e.g., ‘what is the object?’) and recognition (e.g., ‘have I seen that specific object before?’). In line with the hypothesis of multiple-function regional activity, the MUSI account hypothesizes that states 1 and 2 both involve activation in object-sensitive occipitotemporal cortex (Schendan & Kutas, 2007a; Schendan & Stern, 2008).

1.3.1 State 1

The main state 1 hypothesis is the following. In this state, the fast bottom-up pass through this occipitotemporal cortex happens between 95 to 115 ms to around 150 to 250 ms (Fig. 1). In state 1, categorical perception happens along the ventral visual pathway, and this predominantly feedforward information processing in state 1 can be sufficient under unambiguous, optimal conditions to achieve higher cognition (e.g., a decision) in state 2.

1.3.2 State 2

The main state 2 hypothesis is the following. A second state of object knowledge activity takes place between ~150-230 ms and lasting until around 500 ms or later (Figure 2), with timing varying with visual input and task demands. At this time, a sustained state of iterative activation of object-sensitive occipitotemporal cortex involves bottom-up, recurrent, and feedback interactions among these areas and with other brain structures, especially prefrontal and occipitoparietal cortex (David et al., 2005; Fazl et al., 2009; Schendan & Kutas, 2002, 2007a; Schendan & Maher, 2009). In state 2, higher cognition primarily occurs for the first time; that is, cognitive functions associated with actual decision-making (including under ambiguous or impoverished conditions), consciousness (especially phenomenological consciousness), and automatic mental simulation that grounds cognition, memory and meaning in modal information processing.

1.3.3 State M

While initial version of the MUSI account focused on states 1 and 2 (Schendan & Kutas, 2007a; Schendan & Maher, 2009), a third state, M (for multiple network), has been proposed recently (Schendan & Ganis, 2012; 2015). The main hypothesis is the following. In state M, a default mode network accomplishes internal evaluation of decision and memory processes, and

this regulates large-scale cortical network interactions among multiple networks (e.g., frontoparietal control, salience) and can further modulate posterior cortex. In state M, large-scale anti-correlated network activity (e.g., control, salience, and default mode) and their interactions support even higher-order cognitive functions or ‘elaborated cognition’ based on earlier, especially state 2, processing. Default mode network contributions include episodic memory retrieval and encoding, strategic mental imagery or simulation, decision evaluation, divergent thinking for creativity, and access consciousness. State M processing has been considered to be post-decision or post-categorization, with the decision or categorization instead happening earlier in state 2 (Folstein & Van Petten, 2008; J. S. Johnson & Olshausen, 2003, 2005; Ritter, Simson, Vaughan, & Friedman, 1979). State M elaborates on state 2 processes and can influence and change the ultimate final decision, category, or motor behavior, as well as support episodic memory retrieval and encoding and strategic cognitive abilities, such as mental rotation, and other processes of creativity, such as divergent thinking using a default mode network and multiple large-scale network interactions (Vartanian et al., 2018). Accomplishing this can include a third activation of modal processing cortex (state M multiple-function regional activity) where information is processed, stored and encoded, such as in occipitotemporal cortex.

1.3.4 State 2 and M Networks

The frontoparietal regions that predominate in state 2 include those in executive control and dorsal attention networks, which are active task networks that are anti-correlated with the default mode network regions that support the internal evaluation, memory, access consciousness and creativity functions in state M (Spreng, Sepulcre, Turner, Stevens, & Schacter, 2013), further supporting functional dissociations between states 2 and M (Ganis, Schendan, & Kosslyn, 2007; Schendan & Ganis, 2015; Schendan & Kutas, 2003; Schendan & Lucia, 2010; Schendan & Stern, 2007, 2008). However, while the default mode network dominates for the functions so far identified for state M, this state is labeled M because it involves multiple network interactions, and this multiplicity suggests future work will further subdivide state M into multiple states. For example, a slow wave may be better characterized as a late response planning and working memory state (Schendan & Ganis, 2015).

1.4 Consciousness

Debates about the neural architecture of consciousness are independent of this account, but the MUSI account favors the view that recurrent processes and feedback, especially from frontoparietal to posterior cortex, are key to consciousness (Lamme, 2003). In this vein, MUSI proposes that state 2 predominantly supports phenomenological (a.k.a. phenomenal) consciousness, which is brief, susceptible and not readily reportable and associated with iconic sensory memory, and state M predominantly supports access (or report) consciousness, which is readily reportable and associated with working memory. That feedback is key to phenomenological consciousness would make MUSI a higher-order theory of consciousness, and the ideas and evidence for MUSI are consistent with other challenges to first-order theories (H. C. Lau & Passingham, 2007; Ledoux & Brown, 2017). Nonetheless, within the domain of emotion, for which subcortical structures are necessary and have a core role, first-order theories are increasingly compelling and influential in mental health (Alcaro, Carta, & Panksepp, 2017; Panksepp & Biven, 2012) and in comprehensive theories of the brain basis of object cognition, memory, meaning, consciousness, self and embodied cognition (A. R. Damasio, 2010). Whether of cortical or subcortical origin, (a) feedback, reentrant, recursive and recurrent neuronal pathways and (b) synchronous ensembles of such neurons that are bound together for information processing (e.g., object features) have been proposed to be necessary for consciousness (A. R. Damasio,

2010). MUSI thus takes a hybrid view that core or primary modal processing (e.g., state 1) can contribute to some degree of consciousness, but requires certain types of recurrent and feedback processes in the neural architecture and certain environmental circumstances (e.g., stimuli, task) in order to become conscious. MUSI also proposes that different states (e.g., state 1 vs. 2) contribute in different ways to consciousness, as constrained by their recurrent and feedback architectures; the quality (or qualia) of consciousness varies by state. For example, in state 1, feedforward activity triggers automatic recurrent and feedback processes along the ventral visual pathway, and such automatic feedback may support a more rudimentary form of consciousness than is possible in state 2 when feedback also includes frontoparietal contributions (e.g., ‘elementary’ vs. ‘standard’ phenomenological consciousness in states 1 vs. 2, respectively). In such a hybrid version, MUSI hypothesizes that state 2 has a greater role in phenomenological consciousness and can influence access consciousness in state M more than state 1. In short, the quality and qualia of consciousness transform progressively into more advanced and complex forms as processing proceeds from state to state.

1.5 Object Constancy

People can categorize (e.g., a dog) and recognize objects as familiar (e.g., the dog I saw in the park yesterday) fast and accurately. However, their performance can become slower and/or less accurate as sensory information about an object differs more and more from previous experience or the learning situation. Nonetheless, accuracy continues to be good despite remarkably wide variations in sensory input from the original learning experience. For example, people categorize and recognize objects accurately despite unusual viewing angles, poor lighting, far distance, and other impoverished viewing conditions. Critically, however, this accuracy comes at a cost of longer time to respond (Bülthoff, Edelman, & Tarr, 1995; Kosslyn et al., 1994; Palmer, Rosch, & Chase, 1981; Schendan & Ganis, 2015; Srinivas, 1995; Tarr & Pinker, 1989).

How can the brain achieve the perceptual constancy of cognition when visual input poorly matches memory? The MUSI account hypothesizes that later states 2 and M support the ability to categorize objects and recognize them as familiar under widely varying sensory conditions -- that is, the *object constancy* of memory (i.e., similar responses to particular objects despite changes in orientation, size, or other perceptual properties). This is important because, to be most widely utilized, memory or the meaning of a concept (e.g., ‘dog’) should be activated despite widely varying stimuli, such as its name and different perceptual instantiations across sensory modalities (e.g., pictures of dogs under diverse visual conditions, its sound, how it feels). As mentioned, critically, performance is slower when a stimulus provides *impoverished* information, as under ambiguous or nonoptimal sensory conditions (e.g., unusual viewpoints, unfamiliar instantiations, in fog, crowding,). One reason for this slowing is that impoverished images match more poorly to representations in memory, potentially requiring further processing for an accurate solution to the perceptual problem. Further, feature dissimilarity can affect the construction of diagnostic cues used to decide the match of the perceived object to memory (Schyns, 1998). With impoverished images, computational modeling indicates that initial fast bottom-up processing along the ventral visual hierarchy cannot explain human performance levels (Serre, Oliva, & Poggio, 2007). Instead, to do so, theories of *perceptual hypothesis testing* (PHT) implicate top-down feedback contributions (e.g., Gosselin & Schyns, 2001; Grossberg, 1999; Hochstein & Ahissar, 2002; Humphreys, Price, & Riddoch, 1999; T. S. Lee & Mumford, 2003; J. Liu et al., 2011; Lowe, 1985; Lowe, 2000; Ullman, 1995).

1.6 Memory

1.6.1 Multiple memory systems theory

MUSI describes how different kinds of memory are associated with different brain states and how these memory processes support visual cognition, so, next, memory theory is summarized; note, debates about memory theories are independent of MUSI but do inform it, and MUSI favors an embodied cognition framework. According to the *multiple memory systems* theory different kinds of memory depend on different brain systems (Schacter & Tulving, 1994; Squire & Zola-Morgan, 1991). Convergent evidence for dissociations between different kinds of memory has divided a system for ‘*explicit memory*’ that occurs with conscious awareness into 2 systems (Kan, Alexander, & Verfaellie, 2009; Rosenbaum et al., 2005; Tulving, 1972; Vargha-Khadem, Gadian, & Mishkin, 2001; Vargha-Khadem et al., 1997). (1) *Episodic memory* is tied to personally-experienced events, and depends upon the *mediotemporal lobe* (MTL) (Eichenbaum, 2000). For example, episodic memory supports free recall (e.g., of objects on a study list) and recognition of an object from previous experience with it, including feelings of familiarity. (2) *Knowledge memory* supports world facts accumulated over a life time that are not tied to a personal episode, including ‘*semantic memory*’ about the meaning of words and objects and *perceptual representation systems* (e.g., visual object structure) (Warrington, 1982). (3) The knowledge system also supports *semantic*, *conceptual*, and knowledge-based *perceptual implicit memory*, which occurs without conscious effort to retrieve memory. This supports *priming*, which is measured behaviorally as performance differences, typically decreases in response time (RT) or increases in accuracy for repeated relative to new items, and measured neurally as activity differences between these conditions (Gabrieli, Fleischman, Keane, Reminger, & et al., 1995; Gabrieli et al., 1994; Keane, Gabrieli, Mapstone, Johnson, & Corkin, 1995; Keane, Gabrieli, Fennema, Growdon, & Corkin, 1991; Tulving & Schacter, 1990; Verfaellie, Cermak, Blackford, & Weiss, 1990).

The MUSI account hypothesizes that, while priming can have small effects during state 1 under limited, extreme conditions, most types of knowledge and implicit memory occur typically and primarily in state 2, and episodic memory occurs primarily in state M. Research on knowledge has focused on the organization of meaningful (semantic) representations, especially in the context of language, but less work has been done on how perceptual knowledge is matched to stimulus information in order to categorize an object (e.g., how shape activates meaning). The MUSI account addresses this gap by focusing on perceptual knowledge.

1.6.2 Amodal Knowledge in Anterior Temporal Lobe (ATL)

The knowledge system, especially semantic memory, in multiple memory systems theory aligns with the *standard theory of cognition*: Conceptual knowledge is represented in a single *amodal* system (Tulving, 1972) that represents meaning in a symbol system, which has a uniform architecture and resides apart from modal systems for processing specific types of information, such as sensory, motor or emotional information (Fodor, 1983). An amodal system, if it exists, may reside in the ATL (Visser, Jefferies, & Lambon Ralph, 2010), which is widely accepted to support semantic memory, though the precise role is debated (Binney, Embleton, Jefferies, Parker, & Ralph, 2010; Gorno-Tempini et al., 2004; A. C. Lee et al., 2006; Mahon & Caramazza, 2009; Murray, Bussey, & Saksida, 2007; Patterson, Nestor, & Rogers, 2007; Rogers & Patterson, 2007; Simmons & Martin, 2009; K. I. Taylor, Moss, Stamatakis, & Tyler, 2006).

1.6.3 Embodied Memory in Modal Cortex

However, some evidence invalidates strong versions of the standard theory, leading current views of knowledge to incorporate an alternative to a strong standard theory: *embodied (or grounded) cognition* theory that proposes all knowledge depends upon multiple modality-specific systems for sensorimotor “properties”, as in perceptual systems based on the senses (e.g., vision),

action systems for motor planning, emotional and mental state systems (Barsalou, 2008; Chao, Haxby, & Martin, 1999; Devlin, Gonnerman, Andersen, & Seidenberg, 1998; Dilkina, McClelland, & Plaut, 2008; Downing, Chan, Peelen, Dodds, & Kanwisher, 2006; Goldrick, 2008; Kable & Chatterjee, 2006; A. Martin, 2007; McClelland & Rogers, 2003; Moore & Price, 1999; Paivio, 1991; Tyler & Moss, 2001). Different systems support modality-specific, object, word, and face knowledge (Barsalou, 2008); for example, object-sensitive occipitotemporal cortex supports visual object knowledge. The main proposed mechanism for how cognition and memory, including knowledge and meaning, are grounded or embodied in modal information processing is mental simulation, which can be automatic or strategic (Barsalou, 2008, 2009; Glenberg, 1997). Simulation occurs when neural activity in modal association cortex triggers time-locked, recurrent and feedback activity across multiple lower-level modal processing areas, which are the areas from which the memory was initially constructed during the learning experience. Through this distributed multi-regional activity, seeing an object or reading its name (e.g., “dog”) re-enacts associated features that were stored during earlier learning experiences (e.g. its shape, color, motion, actions with it), thereby constructing higher cognition, memory, and meaning. However, debates on the role of embodiment in cognition (Gerlach, 2007; Mahon & Caramazza, 2008, 2009; Patterson et al., 2007) have motivated hybrid proposals, such as those that have both an amodal system and embodied knowledge (e.g., one amodal “hub”; multiple “convergence zones”) (H. Damasio, Grabowski, Tranel, Hichwa, & Damasio, 1996; Patterson et al., 2007). In an embodied cognition framework, MUSI hypothesizes that automatic mental simulation occurs in state 2, whereas strategic simulation occurs in state M.

2 State 1: Details and further evidence

2.1 Object processing along the visual pathways

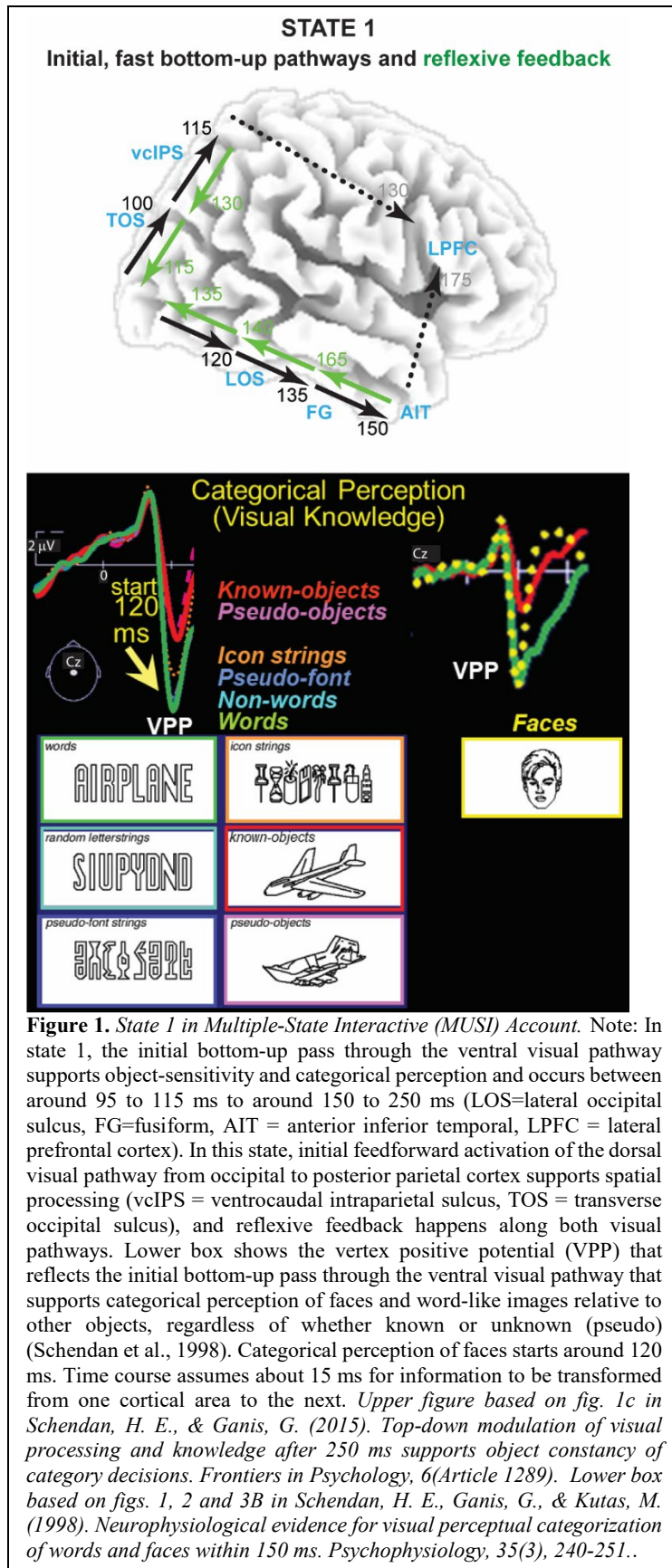
A key hypothesis of the MUSI account is that, under unambiguous or optimal stimulus conditions, processes during state 1 that underlie categorical perception may provide sufficient information to enable later states to compute a decision rapidly with minimal or no additional processing. In state 1, initial activation of object processing cortex feeds forward from occipital to anterior temporal cortex along the ventral stream and from occipital into posterior parietal cortex along the dorsal stream; note, as the feedforward sweep proceeds, this activity automatically triggers reflexive feedback inputs from higher to lower areas, as well as between dorsal and ventral pathways (Bacon-Mace, Mace, Fabre-Thorpe, & Thorpe, 2005; Foxe & Simpson, 2002; Hupe et al., 2001; Hupe et al., 1998; Keyser & Perrett, 2002; Rennie, Robinson, & Wright, 2002), and the ventral pathway processes of interest can be influenced by the dorsal visual pathway, which processes information more rapidly (Bar, 2003).

Like visual cortex in nonhuman primates (Baker, Behrmann, & Olson, 2002; Connor, Brincat, & Pasupathy, 2007; Felleman & Van Essen, 1991; N. Li & DiCarlo, 2008; Olson, 2001; K. Tanaka, 2003), human occipitotemporal cortex shows progressive hierarchical convergence as processing feeds forward from posterior to anterior areas. Along this feedforward pathway, stimulus selectivity becomes increasingly complex from more elementary, local features (e.g., shape or form, color, spatial location, and motion) and greater visual-specificity to higher-order global shapes and combinations of features and increasing visual constancy (Eger, Schyns, & Kleinschmidt, 2004; Grill-Spector et al., 1999; Grill-Spector & Malach, 2004; Hasson, Levy, Behrmann, Hendler, & Malach, 2002; Lerner, Hendler, Ben-Bashat, Harel, & Malach, 2001; Levy, Hasson, Avidan, Hendler, & Malach, 2001; Op de Beeck, Haushofer, & Kanwisher, 2008; K. Tanaka, Saito, Fukada, & Moriya, 1991; Tjan, Lestou, & Kourtzi, 2006). The fast feedforward

sweep through the posterior ventral cortical hierarchy progresses from primary visual cortex in area V1 then to V2 then to V4 and into inferotemporal cortex in nonhuman primates. This well-established hierarchical organization of visual cortex has inspired bottom-up theories of cognition that propose how this feedforward sweep can achieve a category decision (Riesenhuber & Poggio, 1999; Serre, Wolf, Bileschi, Riesenhuber, & Poggio, 2007; Thorpe, Fize, & Marlot, 1996).

The functional organization of occipitotemporal cortex is such that there is systematic variation in cortical location according to the category of the visual image, and so, in the MUSI account, different categories of objects have states that are similar functionally but differ in cortical organization and associated spatiotemporal dynamics (e.g., Schendan & Ganis, 2012). Some areas are specialized for processing broad domains of objects, such as faces, buildings, and body parts (Downing et al., 2006), but categorical organization is experience-dependent (Bukach, Gauthier, & Tarr, 2006; Folstein, Palmeri, Van Gulick, & Gauthier, 2015; Wong, Palmeri, Rogers, Gore, & Gauthier, 2009). In humans, like earlier areas, occipitotemporal cortex is retinotopic, such that adjacent locations in the retina (and corresponding visual field) are represented in adjacent neurons in the cortex. However, at this advanced processing stage, occipitotemporal cortex has a category-specific retinotopic organization such that objects requiring central vision (e.g., faces and word-like images) have center-biased cortical representations, while objects requiring integration across large spatial scales (e.g., buildings) are associated with periphery-biased representations, and objects requiring both central and peripheral vision (e.g., tools) have both central and peripheral representations (Hasson et al., 2002). Occipitotemporal cortex also responds more strongly to images containing objects or object-like structures, including scenes of multiple discernable objects, than images with no coherent object structure in which no figure is discernable (Malach et al., 1995): This ‘object-sensitivity’ is a hallmark of this cortex, which is necessary for normal behavior on a wide range of tasks with objects. For example, patients with occipitotemporal dysfunction have visual agnosia: impaired perceiving, categorizing, and recognizing of visual objects with the pattern of deficits varying with the locus of damage (Behrmann, Peterson, Moscovitch, & Suzuki, 2006; Farah, 1990; Humphreys et al., 1999; Riddoch & Humphreys, 1987; Warrington, 1982).

Across object-sensitive occipitotemporal cortex, in addition to the center-periphery retinotopic organization, the functional cortical architecture is widely distributed and overlapping across category-specific (e.g., face) and general (nonface) areas (Gauthier, Curran, Curby, & Collins, 2003; Gauthier, Tarr, Anderson, Skudlarski, & Gore, 1999; Kanwisher, McDermott, & Chun, 1997; Kriegeskorte, Mur, & Bandettini, 2008; Kriegeskorte, Mur, Ruff, et al., 2008; Op de Beeck, Haushofer, et al., 2008; Schwarzlose, Baker, & Kanwisher, 2005; Yovel & Kanwisher, 2004). Such distributed organization seems to depend substantially on selectivity for visual features (e.g., color, shape, texture, motion, location, size) and visual similarity among objects, which structures perceptual processing and decision-making (Cichy, Kriegeskorte, Jozwik, van den Bosch, & Charest, 2019; Grill-Spector et al., 1999; Jozwik, Kriegeskorte, & Mur, 2016; Kourtzi & Kanwisher, 2001; Op de Beeck, Deutsch, Vanduffel, Kanwisher, & Dicarlo, 2007, 2008; Op de Beeck, Wagemans, & Vogels, 2008). For example, objects within a category tend to be more visually similar to each other than objects from another category, and activity patterns across occipitotemporal cortex show an organization such that objects within a category (e.g., shoes) or a feature (e.g., color) activate a similar set of regions that is distinct but somewhat overlapping with the set of regions activated by a different category (e.g., chairs) or feature (e.g., shape) (e.g., Cichy et al., 2019; Haxby et al., 2001).



2.2 Time course of visual object processing within 250 ms in state 1

In state 1, predominantly bottom-up processes along the visual pathways occurring within 250 ms in humans support object-sensitivity, perceptual grouping and activation of knowledge for categorical perception, implicit learning and implicit memory. Neurophysiological and computational evidence indicates that the initial, fast bottom-up activation of higher-order extrastriate visual areas happens from around 95 ms until around ~170 to 250 ms (David et al., 2006; Schendan & Lucia, 2010). The early P1(00) from 95 to 115 ms indexes occipitoparietal cortex along the dorsal stream for processing spatial information, location, motion, and functional knowledge about objects, and the late P1(00) from 120 to 140 ms indexes occipitotemporal cortex along the ventral stream for processing the shape and color of objects (Di Russo, Martinez, Sereno, Pitzalis, & Hillyard, 2001).

2.2.1 Object-sensitivity and categorical perception within 180 ms

The initial, fast bottom-up activation of human object-sensitive cortex takes place from around 95 ms until around ~155 ms (Craddock, Martinovic, & Muller, 2015; Schendan & Lucia, 2010). Human occipitoparietal cortex along the dorsal visual pathway and occipitotemporal cortex along the ventral visual pathway have been shown to be object-sensitive using standard methods in fMRI, for example, comparing images of real objects and completely phase scrambled versions of them (Schendan & Stern, 2007). ERPs using this fMRI paradigm reveals that the P1(00) (in a large group of people, $N=57$) first begins to differ between the real objects and phase scrambled versions (i.e., shows object-sensitivity) around 95 ms, reflecting processes to achieve figure-ground segregation (Schendan & Lucia, 2010). This object-sensitive neurophysiological activity localizes especially to the right hemisphere in extrastriate occipital cortex in Brodmann's area (BA 18) during the early P1 (95-115 ms) and inferior occipital gyrus in BA 18 during the late P1 (120-140 ms) and lasts until around 155 ms. Furthermore, these areas show reactivation after 200 ms, consistent with the MUSI account of multiple states of activation of the same region. Thus the early P1(00) shows the earliest *object-sensitivity*, which is a hallmark of visual cortical processing of object structure and defines the core object processing areas in fMRI (Schendan & Stern, 2007). However, categorical perception does not yet occur during the P1(00) (Ganis, Smith, & Schendan, 2012).

Instead, the initial bottom-up activation of visual object knowledge in human occipitotemporal areas that supports the earliest categorical perception is revealed in a *vertex positive peak* (VPP), a frontocentral positivity peaking around 150-170 ms, and its polarity-inverted counterpart at occipitotemporal locations, the N170 (Allison, Puce, Spencer, & McCarthy, 1999; David et al., 2006; Joyce & Rossion, 2005; Schendan, Ganis, & Kutas, 1998). From between 120 and ~170 to 200 ms post-stimulus, the VPP/N170, and its magnetoencephalographic (M170)] and intracranial equivalents (N200s and their polarity-inverted P180s) discriminates globally between coarse, behaviorally-relevant object categories, such as a face versus a wide variety of non-face objects (Ganis & Schendan, 2008; Ganis et al., 2012; Schendan & Ganis, 2013; Schendan et al., 1998). The VPP/N170 indexes categorical perception based on expertise with particular image categories, being larger for faces and letter-strings (e.g., words) than other objects, even when perceptually-matched (Allison, McCarthy, Nobre, Puce, & Belger, 1994; Allison et al., 1999; Bentin, Allison, Puce, Perez, & McCarthy, 1996; Ganis & Schendan, 2008; Halgren et al., 1995; Joyce & Rossion, 2005; McCarthy, Puce, Belger, & Allison, 1999; Puce, Allison, & McCarthy, 1999). Spatial configuration and salient face features affect VPP/N170 amplitude and face cognition (Bentin, Golland, Flevakis, Robertson, & Moscovitch, 2006; Flevakis, Robertson, & Bentin, 2008; Gu, Li, Yang, & Zhu, 2007). The VPP/N170 category-specificity has been shown

primarily for faces and words (Schendan et al., 1998), and other objects -- often one category like cars -- were tested mainly for comparison (Itier & Taylor, 2004b; Rossion, Joyce, Cottrell, & Tarr, 2003). Critically, face-specificity holds when comparing faces with a wide variety of object categories and cannot be explained by perceptual interstimulus variance (i.e., faces vary less from each other perceptually than do other objects, e.g., cars) (Ganis et al., 2012; Schendan & Ganis, 2013). Neural processes underlying VPP/N170 have been implicated in learning and representing knowledge for expert object categorization (Curran, Tanaka, & Weiskopf, 2002; Rossion, Curran, & Gauthier, 2002; Rossion, Kung, & Tarr, 2004; Scott, Tanaka, Sheinberg, & Curran, 2006; J. W. Tanaka & Curran, 2001). Convergent evidence localizes the brain sources to occipitotemporal cortex for objects and to face-specific areas in posterior fusiform gyrus, inferior occipital gyrus, and superior temporal sulcus for faces (Bötzel, Schulze, & Stodieck, 1995; Corrigan et al., 2009; Horowitz, Rossion, Skudlarski, & Gore, 2004; Itier & Taylor, 2004c; Jacques et al., 2019; Miki, Watanabe, Kakigi, & Puce, 2004; Puce et al., 1999; Rossion et al., 1999; Schendan et al., 1998; Schweinberger, Pickering, Jentsch, Burton, & Kaufmann, 2002; Watanabe, Kakigi, & Puce, 2003). Computational modelling indicates that feedforward processing from V1 to higher areas along the ventral visual pathway explains the category-specificity of the VPP/N170 (David et al., 2006). This provides critical evidence for the MUSI idea that predominantly feedforward processing and reflexive feedback and recurrent processing during state 1 supports categorical perception.

The VPP/N170 also shows *object-sensitivity*, a hallmark of visual cortical processing of object structure. The VPP/N170 shows object-sensitivity that localizes to posterior fusiform gyrus in BA 37 between about 115 and 180 ms (Schendan & Lucia, 2010). This effect localizes to the occipitotemporal areas that are object-sensitive in fMRI (Schendan & Lucia, 2010; Schendan & Stern, 2007), and intracranial N200s show object-sensitive effects (Allison et al., 1999; Horowitz et al., 2004; Malach et al., 1995; Rousselet, Husk, Bennett, & Sekuler, 2008). Crucially, object-sensitive and categorical perception effects on the VPP/N170 consistently start around 120 ms post-stimulus onset (Ganis et al., 2012; Schendan & Ganis, 2013; Schendan et al., 1998; Schendan & Lucia, 2010), defining the start time for the fast bottom-up pass through human object-sensitive occipitotemporal areas that supports the earliest visual object knowledge activation for categorical perception.

2.2.2 Limited Object Constancy

Evidence suggests that state 1 has limited object constancy, and, instead, processes important for object constancy occur after state 1. First, object constancy entails visually invariant (or tolerant) responses, but the VPP/N170 to faces modulates with changes in visual properties like inversion, eccentricity, size, resolution, and spatial position (Caharel, d'Arripe, Ramon, Jacques, & Rossion, 2009; Kovacs, Zimmer, Harza, Antal, & Vidnyanszky, 2005; Kovacs, Zimmer, Harza, & Vidnyanszky, 2007; Mercure, Dick, Halit, Kaufman, & Johnson, 2008; Rousselet, Husk, Bennett, & Sekuler, 2005), showing limited object constancy. Second, bottom-up accounts of object cognition predict less neural activity for more (*vs.* less) impoverished objects along the ventral visual hierarchy because more impoverished images have fewer visual features and so activate fewer neurons and/or activate each neuron more weakly than less impoverished images. Indeed, by 120 ms, VPP/N170 amplitude is smaller for impoverished or scrambled than for intact houses, faces and other body parts (Horowitz et al., 2004; Jemel et al., 2003; Rousselet et al., 2008; Thierry et al., 2006). N170 impoverishment effects correlate with occipitotemporal fMRI signal (Horowitz et al., 2004), but the fMRI signal in object-sensitive areas is instead higher for impoverished than intact images (not smaller like the VPP/N170) and for more than less

impoverished images (Ganis et al., 2007; Schendan & Stern, 2008), as discussed more under state 2. This suggests that the VPP/N170, but not the fMRI, effects reflect predominantly the initial fast bottom-up pass in state 1, which also shows limited object constancy (i.e., limited ability to compensate for image impoverishment); caveat, more versus less activity does not map directly to more versus less neural activity using electromagnetic measures, ERPs reflect phase-locked activity (Nunez & Srinivasan, 2006) while fMRI does not, and the relation between electromagnetic measures and fMRI is not straightforward with evidence suggesting they reveal different, complementary information (Itthipuripat, Sprague, & Serences, 2019).

2.2.3 Perceptual Grouping and Implicit Learning and Memory within 250 ms

Further evidence that state 1 reflects predominantly bottom-up perceptual computations comes from evidence that an occipitotemporal P2(00) between 150 and 250 ms indexes the Gestalt perceptual grouping process of good continuation and closure (Schendan & Lucia, 2010), and implicit memory for these perceptual processes can transfer from a study experience to a memory test (Schendan & Kutas, 2007a, 2007b). The P200 peaks later than the P1(00) and VPP/N170, consistent with P200 grouping processes capitalizing on earlier figure-ground segregation and categorical perception. Perceptual grouping can entail automatic recurrent and feedback processes along the visual pathway (Lamme & Roelfsema, 2000), consistent with the role of reflexive feedback in grouping during state 1.

Overall, the ERP evidence indicates that object-related perceptual processing in state 1 occurs between 95 ms (starting with the P100) and 250 ms (during the P200). Regarding memory, knowledge for categorical perception occurs between 120 and 170 to 200 ms during the VPP/N170 (Schendan & Ganis, 2013), implicit learning can also modulate the VPP/N170 (Scott et al., 2006), and implicit memory for perceptual grouping processing can occur as early as 150 to 250 ms during the P200 (Schendan & Kutas, 2007b).

2.2.4 Limited Role in Higher Cognition

Thus, state 1 supports detecting salient shapes against a background (object-sensitivity), categorical perception, perceptual grouping, and perceptual implicit learning and memory, but what about higher cognitive processes that compute a decision? Decision making is a core function of cognition (Gold & Shadlen, 2007), and visual cognition and decision making accounts have so far emphasized processing in state 1 before 200 ms for supporting cognition, with some emphasizing bottom-up processing (e.g., Philiastrides & Sajda, 2007; Riesenhuber & Poggio, 1999; Serre, Oliva, et al., 2007; Thorpe et al., 1996) and some positing a role for feedback inputs (e.g., Bar, 2003). However, convergent evidence indicates that, while state 1 contributes information to decisions, these early processes do not compute the decision (Allison et al., 1999; Bentin et al., 1996; David et al., 2006; Minamimoto, Saunders, & Richmond, 2010; Rossion & Jacques, 2008; Schendan et al., 1998; Schendan & Lucia, 2010; Warrington, 1982).

For example, if state 1 computes the decision, then the processes that make up this state should vary with task. To the contrary, the VPP/N170 is largely task-independent (e.g., Cauquil, Edmonds, & Taylor, 2000; Crist, Wu, Karp, & Woldorff, 2007; Ganis & Schendan, 2008; Guillaume & Tiberghien, 2001; Joyce, Schyns, Gosselin, Cottrell, & Rossion, 2005; Mouchetant-Rostaing, Giard, Bentin, Aguera, & Pernier, 2000; Philiastrides & Sajda, 2006; Rousselet, Mace, & Fabre-Thorpe, 2004; Schendan et al., 1998; Smith, Gosselin, & Schyns, 2004). For example, the task goal affects the VPP/N170 minimally, if at all, but has much larger and consistent effects on later ERPs after ~200 ms in response to objects and faces (Philiastrides, Ratcliff, & Sajda, 2006; for review see Rousselet, Gaspar, Wiczorek, & Pernet, 2011; Schendan & Ganis, 2012; e.g., Stahl, Wiese, & Schweinberger, 2010). Indeed, even some extreme task manipulations can have no

detectable effect on ERPs in state 1; for example, no differences in N170 categorical perception effects despite wide variations in task difficulty (e.g., detection of color vs. detection of immediate repetition vs. detection of a fruit/vegetable category, Schendan et al., 1998). Where there are effects in both states 1 and 2, effects can also differ in pattern (Voss, Schendan, & Paller, 2010). Such findings also provide evidence dissociating states 1 and 2, and further evidence for this includes findings that task, mental imagery, memory and attention effects are much larger on later ERPs in state 2 than earlier ERPs in state 1 (Schendan & Ganis, 2012, 2015).

Moreover, if the VPP/N170 were indexing processes underlying higher cognition and decisions, factors affecting cognitive and decision performance should modulate it strongly. To the contrary, the VPP/N170 is typically not modulated by categorization success, and shows short-term adaptation (habituation) and little or no long-term repetition effects related to associative memory (Ganis & Schendan, 2008; Gruber & Muller, 2006; A. Harris & Nakayama, 2007, 2008; Heisz, Watter, & Shedden, 2006; Henson & Rugg, 2003; Henson, Rylands, Ross, Vuilleumier, & Rugg, 2004; Itier & Taylor, 2004a; Jeffreys, 1996; Martens, Schweinberger, Kiefer, & Burton, 2006; Schendan et al., 1998; Schendan & Kutas, 2002, 2003, 2007a, 2007b; Schendan & Maher, 2009; Squire & Zola-Morgan, 1991). Further, tasks that require top-down feedback processes, cognitive control and endogenous attention can modulate the VPP/N170 (Ganis & Schendan, 2008, 2011), but these early effects are much smaller than effects on later ERPs after 200 ms (Schendan & Ganis, 2012). For example, the VPP/N170 is much reduced by adaptation from a recently perceived stimulus (a bottom-up process) but slightly enhanced by sustained visual mental imagery, involving entirely top-down modulation from the frontal lobe (Ganis & Schendan, 2008). However, later ERPs show different patterns and much larger effects (Schendan & Ganis, 2012).

In addition, major cognitive factors (e.g., mental imagery, category decision success, meaning, semantic context) modulate occipitotemporal cortex sensitively in fMRI studies, as well as later ERPs after 200 ms, but do not likewise affect the VPP/N170 (e.g., Ganis & Kutas, 2003; Schendan & Lucia, 2009; Schendan & Lucia, 2010; Schendan & Maher, 2009). These minimal effects on the VPP/N170 stand in contrast with many studies showing robust fMRI effects in occipitotemporal cortex with such manipulations (de Fockert, Rees, Frith, & Lavie, 2004; de Fockert, Rees, Frith, & Lavie, 2001; DeGutis & D'Esposito, 2007; Ganis, Thompson, & Kosslyn, 2004; Henson et al., 2003; Pins, Meyer, Foucher, Humphreys, & Boucart, 2004; Schendan & Stern, 2007, 2008; Stern et al., 1996). Instead, cognitive and task manipulations strongly affect fMRI signal and later ERPs (Guillaume & Tiberghien, 2001).

3 State 2: Details and further evidence

Accounts of cognition and decisions have focused on the initial fast bottom-up sweep with unambiguous sensory information (Philiastides et al., 2006; Philiastides & Sajda, 2007; Ratcliff, Philiastides, & Sajda, 2009; Riesenhuber & Poggio, 1999; Serre, Oliva, et al., 2007), but the MUSI account proposes that higher cognition, including decision-making, occurs for the first time in state 2. In this state, starting between ~150-230 ms and lasting until around 500 ms under common conditions, sustained interactive activation of object processing areas in occipitotemporal cortex involves top-down, recurrent, and bottom-up processes among these areas and with occipitoparietal cortex, and, most critically, with prefrontal cortex (PFC). A central function of this interactive activation is to accumulate evidence (e.g., perceptual information, memory) for a decision or task goal (David et al., 2005; Fazl et al., 2009; Philiastides & Sajda, 2007; Rousselet et al., 2011; Schendan & Kutas, 2002, 2003, 2007a; Schendan & Maher, 2009; Schweinberger, Kaufmann, Moratti, Keil, & Burton, 2007; Ullman, 1996). MUSI and related accounts propose

that higher-order or complex cognition, decisions, fine discriminations, and awareness (e.g., phenomenological consciousness) require additional neural computations involving later local recurrent, feedback and inter-areal contributions to perceptual information processing (Bradski & Grossberg, 1995; David et al., 2005; Enns & Lleras, 2008; Grossberg, 1999; Hochstein & Ahissar, 2002; Lamme, 2003; Lamme & Roelfsema, 2000; T. S. Lee, Yang, Romero, & Mumford, 2002; Lowe, 2000; Mumford, 1992; Treisman, 2006; Ullman, 1995; Yang, Tarr, Kass, & Aminoff, 2019). The initial feedforward sweep through the ventral visual stream does not, itself, compute the actual target or category decision. Instead, based on the information and, presumably, knowledge activated during the initial feedforward sweep, later decision making processes use this information and knowledge to compute the decision in state 2.

A hallmark of state 2 is that this is the first time when lateral PFC (LPFC) modulates posterior processing according to the current behavioral context and goal in order to compute an appropriate mental or behavioral response. Human LPFC has a hierarchical organization of increasingly abstract processing from more caudal to more rostral parts to achieve a mental or overt action (Badre, 2008; Badre & D'Esposito, 2007; Badre, Hoffman, Cooney, & D'Esposito, 2009; Buckner, 2003; Bunge, 2004; Courtney, 2004; Fuster, 2003; Graziano & Aflalo, 2007; O'Reilly, Noelle, Braver, & Cohen, 2002; Petrides, 2005; Postle, 2006; Stern et al., 2000). This system maintains patterns of activity for multiple types of information (e.g., linguistic, visuospatial, object, rules) in functionally distinct neural populations, each of which influences (controls) other areas like occipitotemporal cortex (Bunge, 2004; T. Liu, Pestilli, & Carrasco, 2005; Montojo & Courtney, 2008; Sayala, Sala, & Courtney, 2006). The MUSI account proposes that these later neural computations support selection of information, memory or knowledge for a decision. These state 2 processes are especially important when (a) the task is open-ended (e.g., confrontation naming), (b) basic/entry level (e.g., dog) or even more precise (subordinate level, e.g., collie) access to meaning is necessary, (c) the target has not been pre-cued or specified, or (d) sensory input is less similar to stored knowledge, as when stimuli are impoverished or novel, especially regarding the spatial configuration of features. The task, memory, mental imagery, and attentional orienting in state 2 strongly affect (much more than in state 1) which posterior areas are activated, the level of activation, and how areas interact. Further, the pattern of effects can differ depending upon the particular posterior cortical areas involved, such as face versus object areas (Ganis & Schendan, 2008; Schendan & Ganis, 2012). The MUSI account is consistent with interactive activation and competition models of object naming that posit bidirectional flow among network nodes for visual object knowledge, semantic knowledge, and name knowledge and another node for the decision (Humphreys et al., 1999; Noppeney, Price, Penny, & Friston, 2006). The MUSI account also proposes that State 2 reflects knowledge, meaning, and implicit memory processes. Next, further evidence for these proposals is reviewed.

The MUSI account hypothesizes that state 2 processes are indexed by mid-latency negative ERPs, such as the frontal N2(00) related to cognitive control, frontal N3(00) complex related to visual object processing, and the centroparietal N400 related to semantic processing. This is consistent with similar proposals that, following initial bottom-up perceptual processing (or stimulus registration) during the P1 and VPP/N170, mid-latency ERPs reflect the earliest times when cognitive control and decision-making processes operate, including stimulus selection, information and knowledge retrieval, and categorization functions (Folstein & Van Petten, 2008; Ritter et al., 1979).

STATE 2 ACTIVE TASK NETWORK

Decision, Model Selection & Perceptual Hypothesis Testing (PHT)

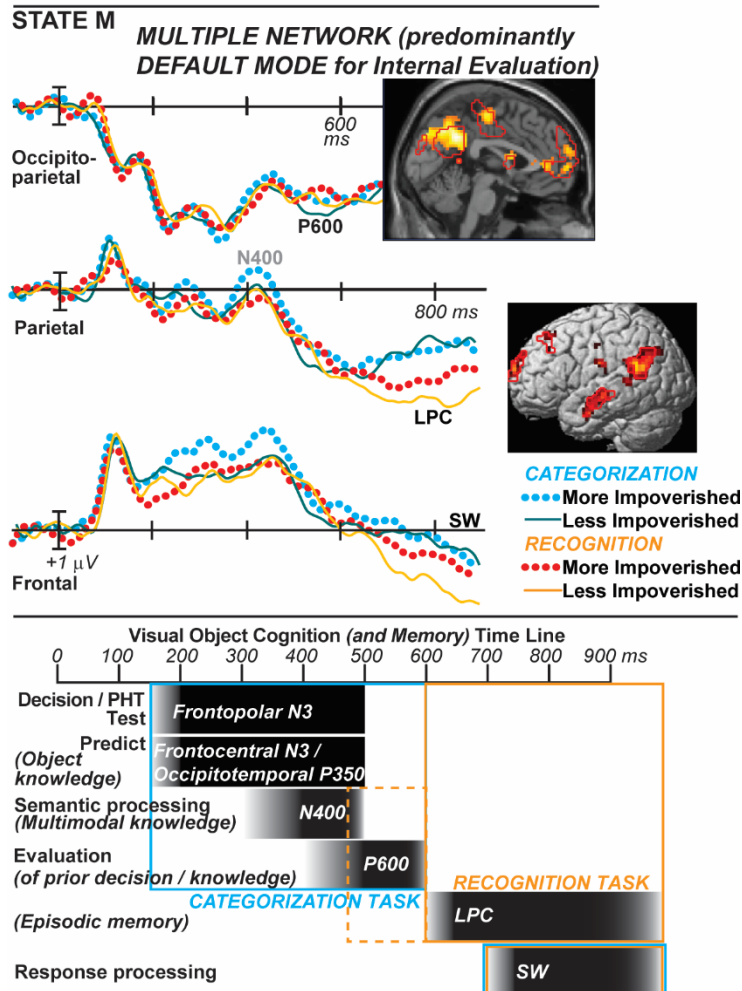
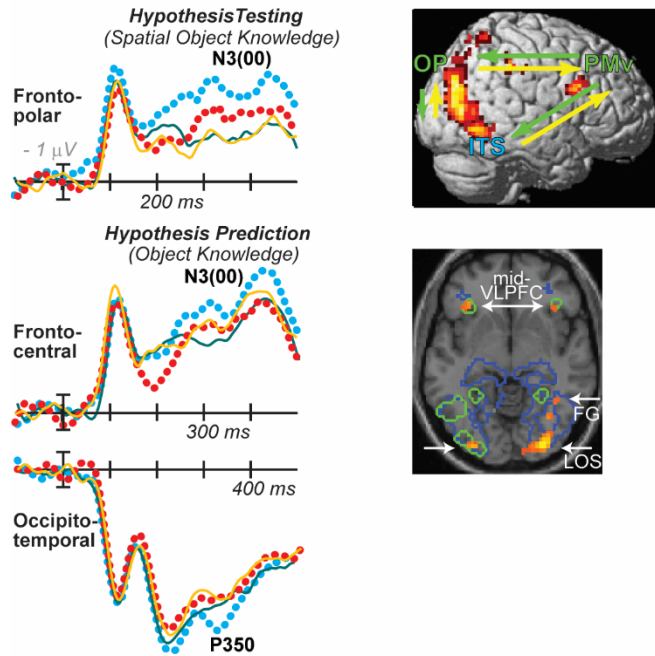


Figure 2. States 2 and M in Multiple-State Interactive (MUSI) Account. Note: Statistical parametric maps on canonical anatomical brains modified from an fMRI study (Schendan & Stern, 2008). Time line (bottom) summarizes the timing of state 2 and M processes and their ERP markers for category decision processes, between about 150-230 ms and lasting until around 500 ms or later in state 2, and after 500 ms for evaluation processes and after about 600-700 ms for episodic recognition processes in state M. STATE 2: Frontopolar N3 shows task-independent impoverishment effects. Likewise for fMRI, the testing system (PMv=caudal ventrolateral prefrontal and ventral premotor cortex (BA 44/6), OP = occipitoparietal cortex, ITS=inferotemporal sulcus) in the active task network is more active for more than less impoverished real objects on both categorization and recognition tasks. Frontocentral N3 shows categorization-specific impoverishment effects. Likewise for fMRI, the prediction system (mid-VLPFC= mid-ventrolateral prefrontal cortex [BA 47/12], LOS=lateral occipital sulcus, FG=fusiform) in the active task network is more active for more than less impoverished real objects on categorization more than recognition. A centroparietal N400 index of abstract semantic memory also shows this pattern. State 2 processes may also support automatic simulation for grounding cognition in modal information processing. STATE M: Like the pattern in parts of the default mode network (medial cortex [retrosplenial, posterior cingulate, medial prefrontal], lateral inferior parietal, and middle temporal gyrus), occipitoparietal positivity from 500 to 600 ms on the P600 shows impoverishment effects on categorization, and, after 700 ms, the late positive complex (LPC) is more positive for less than more impoverished images on recognition more than categorization. Also after 700 ms, the frontal slow-wave (SW), reflecting response related activity or retrieval orientation, shows impoverishment effects (more positive for less than more impoverished images) only on recognition. These later State M processes may also support episodic simulation for grounded cognition. Notably, a slow wave tentatively included in state M may better be characterized in a late response planning state. Figure based on ERP data from Schendan, H. E., Lucia, L. C., & Bridges, D. (submitted). Visual Object Categorization and Episodic Recognition Tasks Recruit Common and Distinct Cortical Processes after 200 ms. Also fMRI figs. 3a, 6, 7 in Schendan, H. E., & Stern, C. E. (2008). Where Vision Meets Memory: Prefrontal-Posterior Networks for Visual Object Constancy during Categorization and Recognition. *Cerebral Cortex*, 18(7), 1695-1711.

Bottom time line shows example time course of state 2 (N3/P3, N400) processes during a category decision task (blue box) and state M processes (P600, LPC, slow-wave) during an episodic recognition task (orange box). The N400-P600 may reflect a transition (orange dotted box) between states 2 and M, whereby semantic memory (e.g., for categorization) increasingly contributes to episodic memory (e.g., for recognition) and active task network activity in state 2 (that predominates for decision-making) transitions to increasing contributions of default mode network activity in state M (for internal evaluation, episodic memory, access consciousness and creativity).

3.1 N3(00) Complex: Cognition and decisions about objects

The N3(00) complex is a negative-going set of ERP components that peak between 200 and 500 ms, typically around 300 to 400 ms, and localize to occipitotemporal cortex (Schendan & Ganis, 2015; Schendan & Maher, 2009; Sehatpour, Molholm, Javitt, & Foxe, 2006; Sehatpour et al., 2008). The N3 has a scalp distribution with an anterior maximum (using references around the mastoid) or the components sometimes show a polarity inversion such that there are simultaneously negative-going waves anteriorly and positive-going waves posteriorly (e.g., a posterior P350 complex, especially using an anterior or common average reference) (Schendan et al., 1998; Schendan & Kutas, 2003; Schendan & Maher, 2009). This scalp distribution is similar to the VPP/N170 (Joyce & Rossion, 2005) with similar implications for underlying brain sources in occipitotemporal cortex. MUSI includes some frontal N2(00) components that are sensitive to perceptual match and cognitive control between 200 and 350 ms (see for review Folstein & Van Petten, 2008) as part of the N3 complex (Schendan & Lucia, 2010; Schendan & Maher, 2009).

Next, key evidence is summarized that the frontal N3(00) complex is the first ERP (and state 2 the first state) to reflect activity in occipitotemporal cortex related to the success of higher visual object cognition and decisions. Like the VPP/N170 (state 1) and fMRI activation, the N3 is object-sensitive, category-specific, and shows adaptation effects (Ganis & Schendan, 2008; Schendan & Ganis, 2012; Schendan & Lucia, 2010). However, unlike state 1 but like occipitotemporal and ventral LPFC (VLPFC) activity captured in fMRI, the N3 varies dramatically with mental imagery and factors affecting category decision success, such as stimulus typicality and impoverishment, implicit memory, knowledge, and meaning (Ganis & Kutas, 2003; Philiastrides & Sajda, 2007; Schendan & Ganis, 2012; Schendan & Kutas, 2002, 2003, 2007a; Schendan & Lucia, 2009, 2010; Schendan & Maher, 2009; Schendan & Stern, 2008; Voss et al., 2010). Crucially, fMRI findings demonstrate that human occipitotemporal cortex shows similar patterns of modulation as the N3, and generally unlike the earlier VPP/N170 (Ganis et al., 2007; Schendan, submitted; Schendan & Lucia, 2012; Schendan & Stern, 2007, 2008). Further, intracranial ERPs between 200 and 400 ms implicate brain sources in VLPFC and occipitotemporal cortex for objects (Allison et al., 1999; Puce et al., 1999), and fMRI effects have been found in VLPFC, posterior parietal, and occipitotemporal cortex for objects in scenes (Gronau, Neta, & Bar, 2008; Henderson, Larson, & Zhu, 2007, 2008; Park, Intraub, Yi, Widders, & Chun, 2007). Intracranial ERPs also indicate that (a) occipitotemporal modulation with categorization success occurs from 228 to 420 ms during state 2, not during earlier P1 and N170 potentials in state 1, (b) LPFC responds to visual objects around 200 ms (Allison et al., 1999), and (c) interactive activity between occipitotemporal and VLPFC regions occurs between 150 to 225 ms and 400 to 475 ms during state 2 (Sehatpour et al., 2008).

Most important, the N3 shows the earliest modulation with factors affecting category decision performance (Schendan & Kutas, 2002; Schendan & Maher, 2009). The N3 is less negative for correct than failed categorization, category members than nonmembers, more than less confidently categorized objects, faster than slower categorization, and categorization of objects with all features rather than missing one or more parts (Doniger et al., 2000; Folstein & Van Petten, 2004; Gratton, Evans, & Federmeier, 2009; Gruber & Muller, 2006; Holcomb & McPherson, 1994; Schendan & Kutas, 2002, 2003; Schendan & Lucia, 2010; Schendan & Maher, 2009). Furthermore, the N3 modulates with perceptual typicality (of a view being unusual vs. canonical, or of an instance or exemplar of a category, e.g., penguin vs. robin), repetition, success of knowledge activation, and visual impoverishment (Ganis & Schendan, 2011; Maher, 2011; Maher & Schendan, 2008; Schendan & Ganis, 2015; Schendan & Kutas, 2003, 2007a; Schendan & Lucia,

2009, 2010; Schendan & Maher, 2009; Schendan & Stern, 2007, 2008; Voss et al., 2010). The N3 modulates with the visual similarity to more global, part-like, shape fragments in a view of an instance of a category (Schendan & Maher, 2009). For example, the N3 shows repetition effects, being larger for new than old repeated objects, that are indistinguishable regardless of whether or not the local lines composing the more global shapes remain the same or differ later on during a memory test compared to the lines composing the object during the learning experience; remarkably, this is true even when no actual lines are shared between learning and test experiences but rather perceptual grouping processes of good continuation and closure between lines enable more global parts and shapes to be perceived (Schendan & Kutas, 2007a). In contrast, when the overall global shape of a particular exemplar of an object category (e.g., this dog) and its more global parts constructed from the lines instead change between learning and memory test (e.g., the object is seen from a different viewpoint or different exemplars, such as two different dog breeds), then N3 repetition effects become smaller relative to when the global shapes and parts remain the same (Maher, 2011; Maher & Schendan, in preparation; Schendan & Kutas, 2003).

3.1.1 Decision-making

Several studies timed visual object knowledge activation on open-ended, Go No-Go, 2-choice, and 4-choice category decision tasks with novel and/or repeated objects. Findings show that the N3 complex is the first ERP to modulate with the success of activating visual object knowledge for the decision (Schendan, 1998; Schendan & Kutas, 2002, 2003, 2007a; Schendan & Maher, 2009). Studies that examined single-trial EEG, corresponding ERPs, and EEG-informed fMRI during perceptual decisions about faces and objects provide additional strong evidence for critical decision processes during the N3 complex but not the earlier VPP/N170 (Philiastides et al., 2006; Philiastides & Sajda, 2006, 2007; Ratcliff et al., 2009; Rousselet et al., 2011). Importantly, this work manipulated both impoverishment (i.e., 6 levels of phase scrambling intermixed randomly) and task (i.e., category vs. color). Activity from 220 to 300 ms during a frontocentral “D220” (D = difficulty), which MUSI considers to be an N3 component, reflects anterior cingulate, frontal eye field, insula, and dorsal LPFC activity related to task difficulty or task differences in cue diagnosticity (Rousselet et al., 2011). More important, activity from 300 to 450 ms, when the N3 typically peaks, reflects interactive activity between VLPFC and object processing areas for accumulating evidence for the decision; notably, both the D220 and a ‘late’ component, which are both N3 components, invert polarity posteriorly, as do N3 components at these times. However, potential limitations of this study include the following considerations: analyses focused on faces and so may not generalize to other objects; exemplars were repeated and so effects are conflated with repetition; simple two-choice decisions were assessed (red or green; face or car Philiastides et al., 2006; face identity 1 or 2 Rousselet et al., 2011) and so results may differ with more open-ended decisions (e.g., confrontational naming); and the category decision required only a superordinate discrimination (i.e., animal or vehicle).

Results from these decision theory studies show that the N3 complex increases while people make category decisions about cars and faces at increasing levels of image impoverishment, and decision-related modulations fit the predictions of decision theory, whereas earlier effects on the VPP/N170 are largely unrelated to performance and reflect only occipitotemporal activity. Work with face images indicates that the N3 but not the earlier VPP/N170 (and EEG at these times) is related to psychometric functions of category decision accuracy and choice probability (Philiastides & Sajda, 2006). Notably, frontal N3 effects are related to the stimuli and RTs (i.e., more impoverished images yield longer RTs) but not motor execution (J. S. Johnson & Olshausen, 2005; Philiastides et al., 2006; Philiastides & Sajda, 2006, 2007; Schendan & Ganis, 2015).

3.1.2 Object Model Selection

The N3 indexes the most critical process for making a category decision, which is ‘*object model selection*’, in which the best match to the percept is activated from among candidate memories (i.e., long-term memory about the visual structure of real objects, e.g., shape, spatial configuration of parts). The N3 complex is the first ERP to differ between perceptually-matched pictures of objects that have been successfully categorized at the entry level relative to those that were unidentified (Doniger et al., 2000; Schendan & Kutas, 2002), decreasing in amplitude with better categorization and naming success. In one approach to timing of visual knowledge, the N3 complex was shown to be smaller for categorized real objects compared to “pseudo” (unknown, unreal) object versions (Kroll & Potter, 1984) with matched visual features (Schendan et al., 1998), or other novel, visual structures (Daffner, Mesulam, Scinto, Acar, et al., 2000; Folstein & Van Petten, 2008; Folstein, Van Petten, & Rose, 2008; Gruber & Muller, 2006; Gruber, Trujillo-Barreto, Giabbiconi, Valdes-Sosa, & Muller, 2006; Holcomb & McPherson, 1994; McPherson & Holcomb, 1999; Sehatpour et al., 2006). Amplitude of the N3 increases as the categorization task becomes more specific (Schendan et al., 1998). Another approach has been to determine the time when ERPs differ with categorization success, which reveals when the brain starts to use knowledge to categorize the object based on the visual input. Findings indicate that model selection based on visual knowledge starts between 175 and 316 ms, depending upon stimulus, repetition, and task factors (Schendan & Maher, 2009).

3.1.3 Implicit memory

Overall, evidence indicates that modulations of the N3 reflect processes for computing a category decision, learning, and implicit memory with objects (Gruber & Muller, 2006; Scott et al., 2006; Sehatpour et al., 2006; Soldan, Mangels, & Cooper, 2006). Regarding memory, the N3 complex shows short- and long-term repetition priming effects on categorization, being smaller for repeated than new objects on tests of implicit memory (Doniger et al., 2001; Ganis & Schendan, 2008; Gruber, Malinowski, & Muller, 2004; Gruber & Muller, 2006; Henson et al., 2004; Schendan & Kutas, 2003, 2007a; Schendan & Maher, 2009). The MUSI account is consistent with synchrony models of repetition suppression and priming (Gotts, 2016). N3 and N400 repetition effects resemble those found in fMRI studies of priming, as well as those in animal models (Brozinsky, Yonelinas, Kroll, & Ranganath, 2005; L. Li, Miller, & Desimone, 1993), that show *neural repetition suppression* – that is, less activity for repeated than new objects (Guo, Lawson, & Jiang, 2007; Henson, 2003); however, the relation between priming and suppression remains to be determined (Desimone, 1996; McMahon & Olson, 2007), with some favoring a link between repetition enhancement and priming instead (Tartaglia, Mongillo, & Brunel, 2014). FMRI, N3 and behavioral repetition priming effects are found for categorized real objects but minimally or none for uncategorized objects, indicating priming specifically of object knowledge and meaning, not merely visual features (Schendan & Maher, 2009; Snodgrass & Feenan, 1990; Voss, Federmeier, & Paller, 2012; Voss & Paller, 2007; Voss et al., 2010). The object knowledge indexed by the N3 complex codes the global shapes of objects and their parts in a specific view, regardless of the constituent local contours composing each shape (Schendan & Kutas, 2003, 2007a). This is consistent with theories that object categorization is based on similarity to part-like, global shape fragments or features in multiple view representations of each object; note, how visual features are represented remains debated (Biederman, 1987; Borenstein & Ullman, 2008; Gauthier & Tarr, 2016; Marr & Nishihara, 1978; Peissig & Tarr, 2007; Ullman, 2007; Ullman, Sali, & Vidal-Naquet, 2001).

3.2 N400: Semantic memory and words

The vast N400 literature has been reviewed extensively elsewhere (Kutas & Federmeier, 2011) so this paper briefly highlights ideas relevant to MUSI. The centroparietal N400 in response to words and other meaningful stimuli is a negative-going ERP with a centroparietal maximum (with mastoid reference) that peaks around 400 ms and shows semantic congruency effects between 300 and 500 ms (Kutas, Federmeier, Staab, & Kluender, 2007; Kutas & Hillyard, 1980). The N400 has been proposed to reflect semantic memory activation related to processing word-related information in anterior temporal cortex and VLPFC (Kutas & Federmeier, 2011). Numerous studies indicate the N400 reflects neural processes involved in representing and/or processing semantic knowledge about words (Van Petten & Luka, 2006). First, N400 amplitude decreases with increasing degree of semantic expectancy for a word in an ongoing sentential context and even in a minimal context, as for semantic priming (i.e., a word pair that shares conceptual information, e.g., doctor-nurse) (Bentin, McCarthy, & Wood, 1985), indicating the N400 is sensitive to the degree to which the semantic information elicited by a stimulus was previously made active (Kutas & Federmeier, 2011). Second, N400 size decreases with higher word frequency (usage), at least for words in isolation (Van Petten, 1993); note these frequency effects at least partly reflect semantic factors, since low frequency words likely symbolize concepts invoked less often. Third, N400 amplitude decreases systematically with repetition (Van Petten, Kutas, Kluender, Mitchiner, & McIsaac, 1991), demonstrating priming. Fourth, fMRI and intracranial ERPs suggest the main generators of the N400 are in VLPFC, especially the BA45 part, and in the ATL and superior temporal gyrus (Friederici, 2002; Halgren et al., 2002; Kutas & Federmeier, 2011; Marinkovic et al., 2003; Nobre, Allison, & McCarthy, 1994; Nobre & McCarthy, 1994, 1995; Patterson et al., 2007; Rossell, Price, & Nobre, 2003; Van Petten & Luka, 2006; Willems, Ozyurek, & Hagoort, 2008).

The MUSI account proposes that the centroparietal N400 indexes later, more abstract, multimodal, associative and complex knowledge processing that may be particularly associated with words, language and analysis of word meaning and semantics. MUSI favors the idea that this more abstract, language-related knowledge is multi, poly, or supra -modal, abstract knowledge (e.g., Chwilla, Virgillito, & Vissers, 2011; Kutas & Federmeier, 2000), which is consistent with an embodied framework, in contrast to being an amodal semantic system described in a standard theory of cognition and memory (e.g., Visser et al., 2010). It is important to emphasize that the N400 can be evoked by stimuli other than words, including pictures of objects, faces, scenes and videos. Future work needs to clarify whether this is due to multimodal abstract knowledge or word-related knowledge processes that are associated with nonverbal stimuli (e.g., the name associated with an object), or both such abstract and word knowledge.

3.3 N400 vs. N3 and amodal vs. embodied cognition

The MUSI account incorporates evidence for the possibility of different knowledge systems for objects and words. Convergent evidence indicates that the frontal N3 complex and centroparietal N400 differ in their posterior neocortical generators based on where knowledge is stored (Thompson-Schill, 2003). While the N3 reflects activity in VLPFC and posterior object-sensitive areas, the N400 localizes to language-related processing areas in VLPFC and posterior middle and anterior temporal cortex and angular gyrus, especially on the left (E. F. Lau, Phillips, & Poeppel, 2008; Marinkovic et al., 2003; Van Petten & Luka, 2006). The N3 and N400 have overlapping functional properties and contributions to state 2 but reflect somewhat distinct neural processes based on their somewhat distinct scalp distributions (Ganis, Kutas, & Sereno, 1996) and response patterns. It is important to emphasize that pictures have been reported to elicit an N400-like ERP, but the scalp distribution tends to be more frontal, like that for the N3 complex, compared

to when words are the stimuli. This raises the possibility that at least part of the frontal contribution to the N400-like ERP to pictures is instead, or in addition, a component of the frontal N3 complex. The MUSI account allows that the frontal N3 complex may include components that do and do not share functional characteristics with the centroparietal N400. MUSI hypothesizes that more frontal N3 components reflect modal visual object knowledge and spatial structure (Schendan & Lucia, 2009), while more central N3 components reflect more abstract knowledge, may be multimodal, have a greater semantic processing role akin to the centroparietal N400 (Ganis et al., 1996).

For example, ERPs in response to real objects or famous faces (e.g., Chaby, Jemel, George, Renault, & Fiori, 2001) show effects of knowledge or semantic congruency with a preceding picture, video or word context, but effects with pictures have a frontocentral maximum, instead of the characteristic centroparietal maximum of the N400 with written words (Bach, Gunter, Knoblich, Prinz, & Friederici, 2009; Ganis & Kutas, 2003; Ganis et al., 1996; Sitnikova, Holcomb, Kiyonaga, & Kuperberg, 2008; Sitnikova, Kuperberg, & Holcomb, 2003). Critically, semantic congruency effects to pictures versus words in sentences have relatively more frontal versus posterior maxima, respectively, but overlapping distributions such that both pictures and their names show some congruency effects at both frontocentral and parietal sites (Ganis & Kutas, 2003; Ganis et al., 1996). Such findings raise the possibility that N400-like picture effects reflect both frontal N3 complex and centroparietal N400 effects, rather than purely N400 semantic processing effects. Both pictures and names may activate both visual knowledge associated with the frontal N3 and more abstract knowledge associated with the centroparietal N400. On the one hand, concrete words that name objects can activate not only their meanings, resulting in N400 modulations, but also associated visual knowledge and other associated knowledge, including embodied information (e.g., sound, action, etc.) through automatic mental simulation mechanisms (Barsalou, 2008; A. Martin, 2007), resulting also in N3 modulations for these words. On the other hand, real objects can activate not only visual knowledge and meanings, resulting in N3 modulations, but also associated names and their word meanings (Humphreys et al., 1999), resulting also in centroparietal N400-like modulations for pictures. Nonetheless, visual memory can be activated independent of abstract and word-related knowledge. For example, visual mental imagery produces frontal N3 effects but little or no centroparietal N400 effects for nonface objects (Schendan & Ganis, 2012), suggesting N3 and N400 effects can dissociate, and pictorial information can activate visual knowledge and mental simulation without activating the semantic and/or word-related processes associated with the centroparietal N400. Consistent with N3 and N400 dissociation, developmental studies show that, while both 8-9 year old children and adults show centroparietal N400 congruency effects, and adults show frontocentral N300 congruency effects for objects and actions, children show the N300 effects only for objects (notably early at 125-300 ms) (Maguire, Magnon, Ogiela, Egbert, & Sides, 2013).

Both pictures and concrete words (e.g., names of objects, such as “dog”) yield similar ERP maxima that lie anterior to those with abstract words (e.g., “freedom”) (Ganis et al., 1996; Holcomb, Kounios, Anderson, & West, 1999; Kutas & Federmeier, 2011). Such findings raise the possibility that both pictures and names activate object knowledge associated with the frontal N3 more than do abstract words. Pictures can automatically also activate semantic processing (Boucart, Humphreys, & Lorenceau, 1995; Pins et al., 2004) and/or word-related processing (e.g., a name) (Humphreys et al., 1999), and, if so, pictures may thus elicit both an N3 component related to visual knowledge and related semantic processing and a centroparietal N400 related to abstract knowledge, semantic and word-related processing. By contrast, abstract words may instead activate semantic processing and/or word-related knowledge associated with the centroparietal

N400 more than do pictures, videos and names, depending upon the particular stimulus conditions and task demands.

Collectively, this evidence suggests multiple systems for knowledge and semantic memory (Ganis et al., 1996), such as those proposed in embodied (grounded) cognition or dual-coding theories (Barsalou, 2008; Paivio, 1991). Intriguingly, N3 effects largely overlap temporally but can start and peak before N400 effects, placing the N3 in a temporal position to reflect processes supporting mental simulation of object information that constructs the meaning analyses indexed by the N400. Consistent with such mental simulation, mental imagery of shape affects the N3 but not the N400 (Schendan & Ganis, 2012). Key additional support for this view comes from evidence that modal perceptual processing of the stimulus affects meaning activation (e.g., Federmeier & Kutas, 2001; Holcomb et al., 1999). This in turn also argues against a sole *amodal* semantic system, for which the most likely ERP index would be the centroparietal N400. Notably, however, the N400 has been proposed to be multimodal, not amodal (Kutas & Federmeier, 2011), and so ERPs have not yet provided evidence for a sole amodal semantic system (e.g., Visser et al., 2010).

In summary, the MUSI account allows for the possibility that there may be multiple semantic systems, and neural sources of the N3 complex to pictures include processes related to visual or unimodal knowledge and semantics, whereas those underlying the centroparietal N400 to words includes processes related to more abstract, multimodal, and language-related knowledge and semantic processing. Evidence suggests that N400-like potentials to pictures may be various combinations of N3 components and the centroparietal N400, not simply the N400 per se. For example, pictures elicit an N3 but may also elicit centroparietal N400-like potentials insofar as word-related, multimodal and/or abstract knowledge or semantic processing is recruited (e.g., name retrieval). On the other hand, N3 components may be elicited by words insofar as visual knowledge or semantics, mental imagery or simulation is activated (e.g., concrete words, sentences emphasizing visual properties).

Nonetheless, it remains also possible that some frontocentral knowledge-related activity in response to nonverbal stimuli like pictures could reflect the abstract knowledge processes associated with the centroparietal N400, but they appear at frontocentral instead of, or in addition to, parietal sites because of somewhat distinct neural generators when the stimulus is a picture instead of a word, such as different regions of VLPFC and the ATL (Gotts, Milleville, Bellgowan, & Martin, 2011; Simmons & Martin, 2009). Given the complexity of the neural architecture for knowledge and semantic memory, sorting out these possibilities will be a challenging but important area for future research because the answers will advance understanding of how memory, knowledge and meaning are constructed across brain regions and computational time. The answers will also determine the precise functions of the neurophysiological activity indexed by the N3 and N400 and the role of these functions in cognition, decisions, memory, meaning and consciousness. Future work should also explore the possibility that the N3 complex includes modal higher-order, knowledge-related semantic processes, and the N400-like response to pictures reflects a combination of both N3 components and centroparietal N400 effects of multimodal abstract knowledge and semantic processing, with the relative contributions varying with the experimental parameters.

3.4 Brain Basis of Top-Down Perceptual Hypothesis Testing (PHT) for Object Constancy

The MUSI account incorporates PHT to explain the brain dynamics for flexibly activating memory for decisions about novel shapes and facilitating the perceptual constancy of object cognition (Schendan & Ganis, 2015). The MUSI account proposes that PHT processes occur first during state 2. Key evidence for this is that category decisions take different amounts of time,

depending upon the stimulus and task demands. ERP negativities after 200 ms reflect this, but not earlier ERPs, including the VPP/N170 index of initial bottom-up activity in occipitotemporal cortex in state 1. Furthermore, bottom-up computational models perform worse than people when the visual system is given or requires more time to accumulate evidence before the decision, as for open-ended categorization (Serre, Wolf, et al., 2007) and highly impoverished stimuli (Ganis et al., 2007; Palmer et al., 1981; Schendan & Kutas, 2003; Schendan & Stern, 2008; Tarr, Williams, Hayward, & Gauthier, 1998). In these cases, people are still accurate, but slower (Potter & Faulconer, 1975): Accuracy costs time. These limitations led some to suggest that the bottom-up pathway provides the initial input and object hypothesis to test using subsequent top-down processes of PHT (Serre, Wolf, et al., 2007). Further, computational modeling increasingly supports a critical role for top-down influences about category knowledge on lower-level cortex (e.g., Yang et al., 2019).

PHT theories propose that top-down inputs facilitate object constancy, but each variant of this type of theory proposes different neural mechanisms. PHT top-down input could originate from within the ventral visual hierarchy itself (i.e., from higher to lower order areas) and/or from other areas, especially parietal and/or lateral prefrontal cortex; see for review Schendan and Ganis (2015). MUSI incorporates a hybrid PHT theory that combines two frontoparietal variants for which convergent evidence indicates PHT processes occur for the first time during state 2, as well as related computational accounts of neural mechanisms; in contrast, most other PHT theories focus on earlier, bottom-up and/or automatic feedback processes during state 1. For this hybrid theory, the main framework comes from *model verification* theory (Kosslyn et al., 1994; Lowe, 1985, 2000), and *multiple-views-plus-transformation* (MVPT) theory provides details about memory representations and spatial processing (Bülthoff et al., 1995; Tarr & Pinker, 1989). Further, neural mechanisms are based on computational models involving hierarchical Bayesian inference (T. S. Lee & Mumford, 2003), adaptive resonance theory (ART) (Fazl et al., 2009; Grossberg, 1999), or predictive coding (Friston & Kiebel, 2009). Convergent evidence supports verification and MVPT variants that are unique in implicating frontoparietal contributions after the initial bottom-up activation of the ventral stream, with PHT processes starting around 250 ms in state 2 (Schendan & Ganis, 2015). These frontoparietal computations are the most important modulators of posterior neocortex in order to achieve object constancy (Ganis et al., 2007; Schendan & Ganis, 2015; Schendan & Lucia, 2012; Schendan, Lucia, & Bridges, submitted; Schendan & Stern, 2008).

According to a hybrid MVPT-verification PHT theory, top-down processes in prefrontal and posterior parietal cortex drive iterative PHT processes to determine the object memory in occipitotemporal neocortex that best explains the percept. When sensory conditions are optimal or for less impoverished images, the percept can be matched to the correct memory (or ‘object model’) and a decision can start to be achieved (state 2) largely, if not entirely, based on information computed by the end of the initial bottom-up pass through the posterior visual processing hierarchy (state 1) with minimal or no additional processing (e.g., Rousselet, Thorpe, & Fabre-Thorpe, 2004). MVPT proposes that multiple views of an object are stored in memory. When an object is observed from a viewing angle that is known, familiar, or canonical (i.e., yields the best performance (Bianz, Tarr, & Bulthoff, 1999; Palmer et al., 1981), the view memories activated during the initial bottom-up pass through the ventral visual hierarchy are sufficient to make a decision (Kosslyn et al., 1994; Tarr & Pinker, 1989).

By contrast, for more impoverished images, the bottom-up pass may find only an initial weak match to visual knowledge about objects (i.e., a weakly activated candidate “visual model”,

hypothesis, or predicted category). Consequently, two top-down PHT processes (Ganis et al., 2007) are recruited that involve cognitive control, working memory, and selective attention functions in frontoparietal cortex (Courtney, 2004; Dolan et al., 1997; Kastner & Pinsk, 2004; Postle, 2006) that interact with and modulate object processing in posterior object-sensitive cortex (Ganis et al., 2007). These two processes cycle iteratively until the task is done (e.g., a decision is made), or fails. Each cycle ends with a “reset” signal to inhibit the rejected hypothesis and allow the next cycle to start (Fazl et al., 2009). (1) The first PHT process is hypothesis ‘prediction’, which predicts the perceptual hypothesis, object model or category that corresponds to the sensory input. Prediction uses the perceptual input and contextual (linguistic or scene) information to find the best match between the perceived object and memory (Ganis et al., 2007; Schendan, submitted; Schendan & Stern, 2008) and may use predictive coding computations (Friston & Kiebel, 2009). (2) The second PHT process is hypothesis ‘testing’, which evaluates the similarity of the spatial configuration of features between the perceived object and the predicted model in memory (Ganis et al., 2007; Schendan & Stern, 2008). The spatial configuration of parts is crucial for object categorization (Behrmann & Williams, 2007; Biederman, 1987; Cave & Kosslyn, 1993). Spatial processes implicated in mental rotation, as posited in MVPT, have been proposed to have a role in testing (Aso et al., 2007; Schendan & Stern, 2007, 2008). According to MVPT, for viewing angles that are unknown, unfamiliar, or unusual, additional spatial processes are recruited to transform and align the perceived image with the view representations in memory to try to achieve a successful match (Bülthoff et al., 1995). Spatial transformation can include frontoparietal processes required for the cardinal spatial task of mental rotation, wherein people decide whether two objects rotated relative to each other are the same or different (Tarr & Pinker, 1989).

Key evidence for a hybrid MVPT-verification PHT theory includes the following. fMRI and positron emission tomography studies have manipulated image impoverishment (e.g., added noise, deleted features, fog). PHT theories predict the opposite of bottom-up accounts for more relative to less impoverished images: PHT processes should show *greater* neural activity (not less, as for bottom-up processes) in object-sensitive occipitotemporal cortex, prefrontal areas for cognitive control (Courtney, 2004; Postle, 2006) and posterior parietal areas for spatial transformation and object mental rotation (Schendan & Stern, 2007). Indeed, findings implicate top-down processes from parietal and LPFC areas (Baird, Colvin, Vanhorn, Inati, & Gazzaniga, 2005; Ganis et al., 2007; Kosslyn et al., 1994; Schendan & Stern, 2008; Sugio et al., 1999). For example, categorizing and recognizing more relative to less impoverished images of objects (fragmented line drawings, unusual views) activates a network of LPFC, occipitoparietal, and occipitotemporal regions, and this impoverishment effect is greater for real than “pseudo-objects” (i.e., unknown or unreal objects), demonstrating the modulation specifically relates to object knowledge (Ganis et al., 2007; Kosslyn et al., 1994; Schendan & Stern, 2008; Sugio et al., 1999). Further, one fMRI study identified task general and categorization-specific processes (Schendan & Stern, 2008).

However, these neuroimaging methods have high spatial but poor time resolution. Using ERPs, which have high time precision, with the same methods as the fMRI studies of object constancy captured the timing of impoverishment effects and task effects (Schendan & Ganis, 2015; Schendan et al., submitted). Regarding timing, this hybrid frontoparietal PHT theory predicts that top-down processes affect occipitotemporal processing after the initial bottom-up pass in state 1 when top-down frontoparietal interactions implement PHT. This predicts impoverishment effects in ERPs (more vs. less impoverished) after ~200 to 250 ms when state 2, top-down frontoparietal modulations and spatial cognition starts or after ~500 ms when effortful

spatial processes that support strategic mental rotation start (Schendan & Lucia, 2009). Consistent with this, the N3 complex is the first ERP to show impoverishment effects: Negativity is greater for more than less impoverished images of real objects (Schendan & Kutas, 2003; Schendan & Maher, 2009). Thus top-down PHT processes facilitate the visual constancy of object cognition for the first time in state 2 during the N3. Consistent with the N3 as an index of top-down processes that activate visual memory, evidence indicates that mental imagery and prior semantic context modulate the frontal N3 (e.g., Ganis & Kutas, 2003; Ganis et al., 1996; Schendan & Ganis, 2012; Schendan & Lucia, 2009; Sitnikova et al., 2008).

Human fMRI and ERP evidence suggests that the two PHT processes operate in state 2 between 200 and 500 ms and suggest where, when and how PHT processes happen. For visual object constancy, neuroimaging implicates VLPFC (Ganis et al., 2007; Schendan & Stern, 2008), which has the most extensive connections with the ventral visual stream (Petrides & Pandya, 2001), a general role in memory retrieval and selection (e.g., Badre, 2008), and a special role in category decisions (Freedman, Riesenhuber, Poggio, & Miller, 2003; Jiang et al., 2007). The MUSI account hypothesizes the following. (1) Prediction involves mid-VLPFC (BA 47/12; BA 45) and *lateral occipital sulcus* (LOS) and right fusiform neocortex along the ventral pathway, and this process is indexed by a frontocentral N390 component of the N3 complex (Ganis & Schendan, 2008, 2011; Schendan & Kutas, 2003; Schendan & Stern, 2008). This neurophysiological activity is task-dependent (e.g., involved in categorization more than episodic recognition, though it has a role in both) (Ganis et al., 2007; Jiang et al., 2007; Kosslyn et al., 1994; Raposo, Han, & Dobbins, 2008; Schendan & Stern, 2008). The BA 47/12 part of VLPFC may predict by flexibly selecting, retrieving, disambiguating and classifying, and actively maintaining visual object information and memory in the LOS until a decision is made (Cisek, 2007; Gotts et al., 2011; Heekeren, Marrett, & Ungerleider, 2008; Kostopoulos, Albanese, & Petrides, 2007; Kostopoulos & Petrides, 2003, 2008a, 2008b; Postle, 2006; Wig, Grafton, Demos, & Kelley, 2005). LOS may predict based on more local features (shape fragments). BA 47/12 in the left hemisphere may have a greater role in linguistic, abstract, local level, or rule knowledge and that in the right hemisphere may have a greater role in nonverbal and global shape information and memory (Badre & Wagner, 2007; Bookheimer, 2002; Bunge, 2004; Dobbins & Wagner, 2005; Ivry & Robertson, 1998; Kan & Thompson-Schill, 2004; Oztekin, McElree, Staresina, & Davachi, 2009; Schendan & Kutas, 2007a; Schendan & Stern, 2008). These object model prediction processes are indexed by a frontocentral component of the N3. In addition, prediction may involve abstract object knowledge, including linguistic knowledge, indexed by the centroparietal N400. This more abstract contribution may reflect a role of BA 45 to predict more abstractly by elaborating retrieved memory selected from posterior memory storage areas, especially the left ATL for linguistic knowledge (e.g., a verbal label) and the right ATL for nonlinguistic knowledge (e.g., perceptual features of an object), extending into surrounding occipitotemporal and parahippocampal regions (Badre & Wagner, 2007; Gorno-Tempini et al., 2004; Marinkovic et al., 2003; A. Martin, 2007; C. B. Martin, Cowell, Gribble, Wright, & Kohler, 2016; Raposo et al., 2008; Thompson-Schill, 2003; Van Petten & Luka, 2006). Accordingly, BA 47/12 connects mainly with occipitotemporal cortex, implicating it in shape prediction, and BA 45 connects mainly with auditory processing areas, implicating it in linguistic and more abstract knowledge prediction (Petrides & Pandya, 2001). Notably, prefrontal cortex, especially VLPFC, may contribute not only to memory retrieval but also to representing conceptual knowledge in a flexible, context-specific way (Gotts et al., 2011).

The model testing process recruits a network involving *ventral premotor parts of a caudal*

VLPFC region (PMv; BA 44/6), an occipitoparietal region, and the *inferotemporal sulcus* (ITS), which are task-independent, showing impoverishment effects on both categorization and episodic recognition (Schendan & Stern, 2008). This is indexed by a frontopolar component of the N3 (a.k.a. N350). The model testing process supports diverse cognitive tasks (e.g., categorization, recognition, mental rotation) (Schendan & Lucia, 2009, 2010; Schendan & Stern, 2008). Accordingly, PMv connects strongly with the intraparietal region (Grezes, Armony, Rowe, & Passingham, 2003), consistent with model testing based on spatial analysis of objects. The occipitoparietal region encompasses 2 retinotopic, object-sensitive areas: the *ventrocaudal intraparietal sulcus* (vcIPS, including area V7) and the *transverse occipital sulcus* (TOS, including area V3A) (Carpenter, Just, Keller, Eddy, & Thulborn, 1999; Denys et al., 2004; Grill-Spector, Kourtzi, & Kanwisher, 2001; Grill-Spector, Kushnir, Hendler, & Malach, 2000; I. M. Harris et al., 2000; Podzebenko, Egan, & Watson, 2002; Sawamura, Georgieva, Vogels, Vanduffel, & Orban, 2005; Schendan & Stern, 2007; Swisher, Halko, Merabet, McMains, & Somers, 2007); note, more anterior intraparietal areas for spatial analysis and object-based properties (Shomstein & Behrmann, 2006) have less of a role in model verification and overlap saccade areas (Schendan & Stern, 2007). The vcIPS is more size- and view-specific and less sensitive to repetition than occipitotemporal cortex, (Grill-Spector et al., 1999; James, Humphrey, Gati, Menon, & Goodale, 2002; Sawamura et al., 2005; Schendan & Stern, 2008; Sugio et al., 1999; Vanrie, Beatse, Wagemans, Sunaert, & Van Hecke, 2002), though TOS shows position-invariant adaptation (MacEvoy & Epstein, 2007). The occipitoparietal region has been implicated in mental rotation, visual working memory (or visual short-term memory) for automatically tracking the relative spatial location of features within an object, object grouping and object-based representation (“object files”), individuating objects, and binding features into an object token representation (Epstein, Harris, Stanley, & Kanwisher, 1999; Epstein & Kanwisher, 1998; Friedman-Hill, Robertson, & Treisman, 1995; Kim & Robertson, 2001; Oztekin et al., 2009; Robertson, 2003; Schendan & Stern, 2007, 2008; Turriziani, Carlesimo, Perri, Tomaiuolo, & Caltagirone, 2003; Wendelken, Bunge, & Carter, 2008; Xu, 2008; Xu & Chun, 2006, 2007). The ITS shows impoverishment and mental rotation effects consistent with a role in model testing and may contribute information and memory about the spatial configuration of features (Schendan & Stern, 2007, 2008). Accordingly, the vcIPS region modulates neuronal activity in more ventral cortex, such as ITS, in ways that fundamentally affect the object representations (Aviezer et al., 2007; Friedman-Hill, Robertson, Desimone, & Ungerleider, 2003; Ganis et al., 2007; McCloskey, 2004), and monkey ventral parietal cortex projects to inferotemporal area TE, which exhibits both shape and spatial configuration properties (Messinger, Squire, Zola, & Albright, 2005; Zhong & Rockland, 2003). Notably, both prediction and testing regions are also recruited for the top-down, spatial mental imagery task of object mental rotation (Aso et al., 2007; Schendan & Stern, 2007, 2008), implicating PHT processes in mental rotation, and vice versa.

Prediction-testing cycles iterate in state 2 during the N3 complex, but PHT can start with testing because the initial bottom-up activation can compute the first prediction (Serre, Wolf, et al., 2007). For more impoverished objects, since the first prediction is likely poor, the first test determines that this predicted model only weakly matches memory and so recruits the first model prediction attempt using PHT processes in state 2. This sequence (i.e., bottom-up yields the first prediction – first test – second prediction then iterative prediction-testing) is consistent with the observation that frontopolar N3 effects (testing) start and peak earlier than frontocentral N3 effects (prediction). However, if the bottom-up pass fails to yield a prediction, then prediction should precede testing, leading to variation in timing of N3 components depending on the situation.

Evidence indicates that knowledge underlying the N3 has a greater role in object constancy than the knowledge underlying the N400, and the semantic activations indexed by the N400 have less of a role in category decisions than perceptual knowledge associated with the N3 complex. FMRI and N3 viewpoint effects indicate greater processing of more (unusual) than less (canonical) views, consistent with frontoparietal PHT accounts of object constancy (Ganis et al., 2007; Schendan & Ganis, 2015; Schendan & Kutas, 2003; Schendan et al., submitted; Schendan & Stern, 2008). The N400 shows small viewpoint effects, being larger for unusual than canonical views during categorization of real objects from ~390 to 500 ms (Schendan & Kutas, 2003). This suggests that word-related semantic processing underlying the N400 has a role in prediction for PHT or N400 semantic processing includes visual knowledge, perhaps as part of its multimodality. However, such effects are not reliable and vary by task, being undetectable on an episodic recognition task (Schendan & Lucia, 2012; Schendan et al., submitted). Regardless, this suggests that, relative to knowledge processes underlying the N3 complex, semantic processes underlying the N400 have a minimal role in episodic recognition and less of a role in categorization. This is consistent with evidence that mediotemporal damage impairs episodic memory and a late positive complex associated with episodic memory in state M, but the N400 remains largely unaffected, being instead abnormal in people with damage to neocortical association areas (J. R. Taylor & Olichney, 2007).

3.5 N3(00) Components & Brain Basis Support Functional Significance of State 2

Next, studies of the N3 complex are reviewed that further explain the functional significance and properties of state 2, dissociations between states and between frontopolar and frontocentral N3 components. Convergent evidence suggests that the N3 is a complex of functionally-distinct components with different cortical sources (e.g., Schendan & Maher, 2009; Sehatpour et al., 2006).

3.5.1 Target N250: Ultra-Rapid Categorization starting by 170 ms (Decisions Based on Initial Bottom-Up Pass)

The ‘target N250’ marks the transition between state 1 and 2 when processing switches from predominantly bottom-up to predominantly recurrent, feedback, top-down and interactive processes that operate according to the task goal. One important source of evidence for this transition comes from ERP studies that aimed to determine the timing of categorization based on the initial bottom-up pass through the ventral visual stream using ‘ultra-rapid categorization’ tasks, on which performance is fastest (~420 ms), compared to other tasks. These studies primarily used tasks involving two-choice decisions about the global “target” category of an object (e.g., animal or not). Subjects are instructed to respond to the target category in complex natural scenes, then the scenes are flashed briefly (20-40 ms) followed by a visual mask (Delorme, Richard, & Fabre-Thorpe, 2000). Subjects report whether the target was present.

The processing difference between targets and non-targets can be detected in the ERPs with an onset at the earliest of between 154 and 170 ms, modulating a ‘target N250’, a negative-going ERP peaking around 250 ms with a maximum at frontocentral locations. The N250 is less negative to scenes where the target category is successfully detected, as indicated by a “Go” RT, relative to when the target is absent, indicated by no response (“NoGo”) (Bacon-Mace et al., 2005; Fabre-Thorpe, Delorme, Marlot, & Thorpe, 2001; Thorpe et al., 1996; R. VanRullen & S. J. Thorpe, 2001). The target effect has been shown not to be attributable merely to feature, motor, category level, and masking factors, but the target effects depend on cognitive and task demands (Bacon-Mace et al., 2005; Delorme et al., 2000; Fabre-Thorpe et al., 2001; J. S. Johnson & Olshausen, 2003, 2005; R. VanRullen & S. J. Thorpe, 2001): The N3 is larger with (i) two-choice than go-no go tasks, (ii) RTs that are faster than slower, (iii) multiple than single category tasks,

and (iv) categorization at the basic level (e.g., dog) compared to a more general, superordinate level (e.g., animal). The brain source of the N250 target effect, which was measured between 190 and 215 ms, has been localized to occipitotemporal cortex (Delorme, Rousselet, Mace, & Fabre-Thorpe, 2004; Fize, Fabre-Thorpe, Richard, Doyon, & Thorpe, 2005). This has been widely accepted as strong evidence that decisions about real objects in complex scenes can be accomplished primarily using powerful discriminative information computed in the initial feedforward sweep along the visual hierarchy from lower-level occipital to higher-level temporal cortex in humans by the 154 to 170 ms onset of the target N250 effect (Fabre-Thorpe et al., 2001; Riesenhuber & Poggio, 2002, 2004; Rolls, Tovee, & Panzeri, 1999; Schoenfeld et al., 2003; Thorpe et al., 1996; VanRullen & Koch, 2003; R. VanRullen & S. Thorpe, 2001). Critically, this onset time is 30 to 50 ms later than the 120 ms start time of categorical perception during the VPP/N170 in state 1, which shows no evidence of a target effect. Thus, the target N250 effect is too late to capture the initial bottom-up activation of the human ventral visual pathway, which instead is captured by the earlier VPP/N170 effects of categorical perception starting at 120 ms. Notably, studies have implicated interactions among top-down prefrontal feedback and bottom-up processes in fusiform cortex as early as 180 ms in visual object cognition (Bar et al., 2006), but these are small, specialized effects. Moreover, 180 ms and the 154 to 170 ms onset of target N250 responses are still long after the 120 ms onset of VPP/N170 effects of categorical perception.

The location, time course, and functional characteristics of the target N250 indicate it is a component of the frontal N3 complex, possibly the earliest part of the frontocentral N3 component, and, according to the MUSI account, the onset of the target N250 during ultra-rapid categorization tasks pinpoints the end of the initial bottom-up pass through the ventral stream (state 1) and the start of decision and other higher cognitive processes (state 2). Convergent evidence indicates that state 1, indexed by early ERPs (e.g., VPP/N170) between 120 ms until around 170 to 250 ms, involves predominantly bottom-up computations, and, starting around 154 to 170 ms, in state 2, processing becomes increasingly dominated by interactive recurrent and feedback processes (e.g., task goal information feeding back from PFC to posterior cortex). For example, top-down prefrontal influences modulate the target N250 (Delorme et al., 2004), and N250 effects reflect ‘post-sensory decision processes’ (J. S. Johnson & Olshausen, 2003, 2005).

3.5.2 Open-Ended Category Decisions Involve Recurrent and Feedback Processes

When the decision is open-ended or sensory input is impoverished or ambiguous (see Sections 1.5 and 4.1), then additional processes are necessary. People are much faster at categorizing objects when the target class is pre-specified (Potter & Faulconer, 1975), as on ultra rapid tasks, than when they must discern the relevant category themselves. Ultra-rapid target detection tasks minimize critical, neural computations that are normally used on “open-ended” decision tasks, such as basic or entry level categorization (e.g., during confrontational naming or when meaning or semantic memory is task-relevant). On open-ended tasks, the visual system has to discriminate one specific class of visual objects from all others with little or no advance information to cue the category (Enns, 2004). Fast bottom-up, hierarchical processing in occipitotemporal cortex is necessary for perceiving the object (Ganis & Schendan, 2008; Horowitz et al., 2004), but this may not be sufficient for a decision, nor for higher cognition or awareness, motivating the MUSI proposal that these happen in state 2.

3.5.3 Frontopolar vs. Frontocentral N3s

In the MUSI account, frontopolar N3s reflect decision processes involving spatial information about objects and hypothesis testing, whereas frontocentral N3s reflect decision or significance-determining processes involving nonspatial, salient feature, semantic or associative knowledge,

and hypothesis prediction.

3.5.3.1 Frontopolar N3: Visual spatial object structure

Effects of novel visuospatial structure (e.g., real vs. pseudo objects) are largest on an N3 component from 200-500 ms maximal at frontopolar locations. The frontopolar N3 component decreases as the percept is rated as a better match to object knowledge (Schendan & Maher, 2009). Notably, this relationship is consistent with an embodied knowledge account of categorization in which perceptual similarity has a crucial role (Goldstone, 1994; Goldstone & Barsalou, 1998; Kruschke, 2008; Shepard, 1987), and evidence that shape similarity drives occipitotemporal activity (Freedman, Riesenhuber, Poggio, & Miller, 2001, 2002; Freedman et al., 2003; Jiang et al., 2007; Kriegeskorte, Mur, Ruff, et al., 2008; L. Li et al., 1993; Op de Beeck, Wagemans, et al., 2008; Rainer & Miller, 2000; Sigala, 2004; Sigala, Gabbiani, & Logothetis, 2002; Sigala & Logothetis, 2002). The N3 has a frontopolar maximum for effects that a hybrid MVPT-verification PHT theory hypothesizes involves more spatial processing in the testing system: (a) impoverishment effects during categorization, (b) repetition and category decision effects with more impoverished objects (Schendan et al., 1998; Schendan & Kutas, 2002, 2003, 2007a; Schendan & Maher, 2009), and (c) stimuli that are relatively atypical or structurally novel for a category (Folstein & Van Petten, 2004, 2008; Folstein et al., 2008; Gratton et al., 2009; Schendan & Kutas, 2003; Schendan & Lucia, 2009; Schendan & Stern, 2007, 2008). Further, an ERP version of an fMRI study of object mental rotation dissociated N3 components: Frontopolar N3s between 200 and 700 ms show robust linear rotation effects like those in occipitoparietal parts of the testing system for PHT, whereas frontocentral N3s do not (Schendan & Lucia, 2009). Overall, evidence also suggests the frontopolar N3 indexes automatic mental simulation to embody cognition in the visuospatial configuration of an object during state 2.

3.5.3.2 Frontocentral N3: Visual feature, object and semantic information, knowledge and memory

In contrast, the N3 has a frontocentral maximum (e.g., N390) between 200 and 500 ms for semantic congruency effects with visual objects for which negativity becomes less when the category has been predicted by a preceding sentence or picture context (Barrett & Rugg, 1990; Ganis & Kutas, 2003; Ganis et al., 1996; McPherson & Holcomb, 1999; Schendan & Maher, 2009; Sitnikova et al., 2008; Sitnikova et al., 2003). When specified using a scene context, semantic congruency effects for objects show a frontocentral N3 but no such frontopolar effect (Ganis & Kutas, 2003), dissociating these components. Frontocentral N3 effects of category decisions and image impoverishment are task-dependent, reflect interactions between the right VLPFC (BA 47/12) and occipitotemporal cortex, especially the LOS (Schendan & Lucia, 2012; Schendan et al., submitted; Schendan & Stern, 2008). MUSI thus proposes the frontocentral N3 indexes the network for a PHT prediction process. Consistent with this, the prediction system for PHT has been implicated in deciding the category of an object using conceptual knowledge (Jiang et al., 2007; A. Martin, 2007; Schacter, Wig, & Stevens, 2007). Thus category decisions involve the PHT prediction network; note, how to link neural data to decision theory remains uncertain, with some suggesting that PMv and vcIPS (indexed by the frontopolar N3) are more important than VLPFC (Gold & Shadlen, 2007; Heekeren et al., 2008; Philastides & Sajda, 2007; Ploran et al., 2007; Ratcliff, 1978; Wheeler, Petersen, Nelson, Ploran, & Velanova, 2008).

Some of the same factors that affect the centroparietal N400 to word stimuli also modulate frontal N400-like ERPs to pictures of non-linguistic visual objects, which herein are suggested to include frontocentral N3 components (see also section 3.3). First, the N400 amplitude to pictures of living and nonliving objects decreases when preceded by semantically-related words and

sentences (Federmeier & Kutas, 2001; Ganis et al., 1996; Kiefer, 2001). Second, the frontocentral N3 and centroparietal N400 decrease when the identical famous face is vividly imagined (cued by its name) before the picture is presented, but nonface objects show only N3 complex effects (Schendan & Ganis, 2012), indicating stimulus-dependence of effects. Third, frontal N400-like ERPs are also modulated by non-linguistic visual contexts: single objects (Barrett & Rugg, 1989, 1990; Holcomb & McPherson, 1994; McPherson & Holcomb, 1999), scenes (Ganis & Kutas, 2003), and video clips (Sitnikova et al., 2008; Sitnikova et al., 2003). In line with these priming effects, the N400-like object congruency effect is accompanied by behavioral semantic priming, that is, faster RTs for objects categorized following a semantically predictive than nonpredictive scene context (Ganis & Kutas, 2003).

Compared to the centroparietal N400 to words, picture effects have a frontocentral scalp distribution and overlapping time course yet can start and peak earlier, resulting in labels like N300 (McPherson & Holcomb, 1999) and frontocentral N390 (Ganis & Kutas, 2003) (i.e., components of the N3 complex). For example, semantic congruency effects at frontocentral head locations with pictures can start and peak earlier than those at centroparietal N400 locations with words (Ganis & Kutas, 2003; Ganis et al., 1996); note, with pictures of objects, the centroparietal N400 can occur or peak later, for example, appearing as an “N450” (e.g., Barrett & Rugg, 1990; Sitnikova, West, Kuperberg, & Holcomb, 2006). In particular, centroparietal N400 linguistic effects reliably start by 250 to 300 ms and semantic effects start by 300 ms (Laszlo & Federmeier, 2014). Most important, when congruency effects in sentences are compared directly for perceptually-matched line drawings of objects and words (Ganis et al., 1996), both peak around the same time (410 vs. 416 ms, respectively) when presented in separate blocks. However, when intermixed, N400-like ERPs peak earlier for pictures than words (397 vs. 414 ms, respectively, with the largest picture advantage (30 ms) at parietal sites. Moreover, only for pictures, the congruency effect starts around 150 ms and is significant between 150 and 275 ms (earlier than with words) at frontocentral N3 sites but not at centroparietal N400 sites (Ganis et al., 1996). Thus semantic congruency effects for pictures relative to words can start up to 125 ms earlier due to early effects only for pictures at frontal N3 sites and can peak earlier at both frontal N3 and centroparietal N400 sites. Further, for pictures relative to words, visual knowledge and abstract semantic processes can not only start earlier but also have a faster time course of processing. This places the visual knowledge underlying the frontal N3 complex in a temporal position (potentially earlier yet overlapping) to embody, mentally simulate and otherwise contribute to constructing meaning using more advanced, multimodal and abstract knowledge and semantic processes during the centroparietal N400. Overall, evidence suggests functional similarity but anatomical differences between word vs. object knowledge (and associated semantic processes) underlying the linguistic centroparietal N400 vs. frontocentral N3, respectively.

Semantic priming links these studies on word and object knowledge to those on ultra-rapid categorization (see also section on ‘Target N250: Ultra-Rapid Categorization by 170 ms’). In standard semantic priming paradigms, exposure to an item, the “prime”, a brief time before (i.e., < about 1 s) improves performance with the next item, the “target”, which it resembles in meaning but not in sensory form (e.g., the word “dog” and then a picture of a dog). From a memory standpoint, both semantic congruency and ultra-rapid categorization include key elements of semantic priming paradigms: The “prime”, which is presented just beforehand, affects subsequent processing of the semantically-related word or picture “target”; for semantic congruency paradigms, the prime is a linguistic or picture context, and the target stimulus is a word or object; for ultra-rapid categorization, the prime is the name of a category (e.g., “animal”), and the target

stimulus is a complex scene of objects, which includes the target (e.g., an animal) or not. Indeed, some ultra-rapid categorization studies used a “name verification” task involving a semantic priming paradigm: A name (e.g., “dog”) primes the subsequent target object in the scene context, and subjects verify the scene as containing the named target or not (J. S. Johnson & Olshausen, 2003, 2005). ERP negativity decreases to scenes with the target (i.e., the primed object) relative to those without it, between ~150 and 500 ms. This ‘target N250’ has the waveform, timing, and scalp distribution of the frontocentral N3 component (J. S. Johnson & Olshausen, 2003), contributing to the earliest part of this N3. Studies that manipulated the original ‘ultra-rapid’ task and the name verification variant demonstrated that these effects cannot be attributed merely to feature, motor, category level, and masking confounds, but some factors in the ‘ultra-rapid’ paradigm minimized the ERP effect, as follows. (a) Backward masking likely minimized top-down processing (Di Lollo, Enns, & Rensink, 2000; Enns, 2004; Enns & Di Lollo, 2000; Enns, Lleras, & Di Lollo, 2006). (b) Categorization at the superordinate level (animal) results in a smaller N3 and smaller target effects than at the basic level (dog), indicating that better prediction reduces the N3. (c) The easy Go-No Go task (in the seminal ultra-rapid experiments) results in an N3 that is earlier and smaller, and RTs that are faster, relative to the 2-choice task used for name verification (Gomez, Ratcliff, & Perea, 2007). (d) Target N250 effects with a single category are much smaller than with many categories; (Ganis & Schendan, 2008; Rossion et al., 2002; Schendan et al., 1998; Scott et al., 2006; J. W. Tanaka & Curran, 2001). Results also show the following. (e) Image impoverishment (e.g., part deletion) decreases and delays the target N250 effect, which is smaller and later when RTs are slower, consistent with findings that the frontocentral N3 indexes PHT processes of prediction for object constancy (Ganis et al., 2007; Schendan & Kutas, 2003; Schendan & Stern, 2008). (f) The centroparietal N400 to words typically also shows these effects, as expected if the word prime activates both name (N400) and object knowledge (N3). Altogether, ERP studies using semantic priming paradigms demonstrate that prediction of object knowledge reduces the frontocentral N3 index of a VLPFC-posterior object-sensitivity network, and improves object memory activation.

3.5.3.3 PHT: Frontopolar N3 indexes testing and frontocentral N3 indexes prediction

The MUSI account proposes that state 2 also contributes to PHT, but the frontopolar N3 indexes testing and frontocentral N3 indexes prediction. Accordingly, the N3 complex is the first ERP to show impoverishment effects: Negativity is greater for more than less impoverished images of real objects (e.g., unusual than canonical views, and more than less fragmented line drawings, respectively) between 200 and 500 ms (Schendan & Ganis, 2015; Schendan & Kutas, 2002, 2003; Schendan & Maher, 2009); note, the centroparietal N400 also shows an effect in some studies (Schendan & Ganis, 2015; Schendan & Kutas, 2003). Frontopolar and frontocentral N3s show the same modulations with key exceptions that implicate the frontopolar N3 as an index of PHT testing. (a) The frontopolar N3 can show less or no effects of object congruency and semantic priming, as opposed to the larger and consistent effects on the frontocentral N3 (Ganis & Kutas, 2003). (b) The frontopolar N3, but not the frontocentral N3, shows linear modulations with categorization success (Schendan & Maher, 2009). (c) The frontopolar N3, but not the frontocentral N3, from 200 to 400 ms shows sustained linear effects of object mental rotation like those found in the occipitoparietal region of the testing system using fMRI (Cohen et al., 1996; Podzebenko et al., 2002; Podzebenko, Egan, & Watson, 2005; Schendan & Lucia, 2009; Schendan & Stern, 2007). (d) The frontopolar N3 to a picture (of a real object or famous face) decreases when preceded by vividly imagining that same picture (cued by its name) relative to a different picture (Schendan & Ganis, 2012). This suggests that the PHT testing network is a brain source of

the frontopolar N3.

Prediction is indexed by the frontocentral N3. Accordingly, evidence indicates that prediction of visual object knowledge improves categorization and reduces the frontocentral N3, which localizes to VLPFC and LOS, and the pattern of frontocentral N3 effects resemble those for the centroparietal N400. Key evidence includes the following. (a) The frontocentral N3 (a.k.a. N390) to visual objects decreases when preceded by semantically-related words and sentences (Federmeier & Kutas, 2001; Ganis et al., 1996; Kiefer, 2001), which may involve semantic priming. (b) The frontocentral N3 to a picture of a famous face decreases when preceded by vividly imagining that same face (cued by its name) relative to a different picture (Schendan & Ganis, 2012). This may be a neural correlate of perceptual repetition priming of categorization performance mediated by visual mental imagery of the prime (McDermott & Roediger, 1994) and/or a mechanism of mental simulation (Schendan & Ganis, 2012). (c) The frontocentral N3 and RTs decrease for objects categorized following a semantically predictive than nonpredictive, non-linguistic, visual context specified using a single object (Barrett & Rugg, 1989, 1990; Holcomb & McPherson, 1994; McPherson & Holcomb, 1999), a scene (Ganis & Kutas, 2003), and a video clip (Sitnikova et al., 2008; Sitnikova et al., 2003). Such scene congruency effects implicate attention processes and the known spatial relations among objects in a scene, and the congruency of the visual knowledge in terms of the spatial position, size, and statistical probability of co-occurrence of the object in the scene (Biederman, 1972, 1981, 1995; Biederman, Bickel, Teitelbaum, & Klatsky, 1988; Biederman, Glass, & Stacy, 1973; Biederman, Mezzanotte, & Rabinowitz, 1982; Biederman, Rabinowitz, Glass, & Stacy, 1974; Biederman, Teitelbaum, & Mezzanotte, 1983). (d) The frontocentral N3 shows the earliest target effect (a.k.a. N250; see Section 3.5.1) in ultra-rapid categorization studies, which use a semantic priming variant in which a name (e.g., “animal”, “dog”) primes the category of a target object (Potter & Faulconer, 1975) in a scene context. This frontocentral N3 is smaller to scenes with the target than without it from ~150 ms until ~500 ms (Bacon-Mace et al., 2005; Delorme et al., 2000; Fabre-Thorpe et al., 2001; J. S. Johnson & Olshausen, 2003, 2005; R. VanRullen & S. J. Thorpe, 2001). (e) Crucially for an index of model prediction, impoverishment decreases and delays frontocentral N3 effects (Schendan & Ganis, 2015; Schendan & Kutas, 2002, 2003; Schendan & Maher, 2009). (f) The frontocentral N3 seems to be generated in VLPFC and occipitotemporal cortex, based on intracranial ERPs from 200 to 400 ms with a mean latency of 250 ms (Allison et al., 1999; Puce et al., 1999), localization of the frontocentral target N250 (measured at 190-215 ms) on ultra rapid categorization tasks to occipitotemporal cortex (Delorme et al., 2004; Fize et al., 2005), similar patterns of fMRI effects in VLPFC and LOS for objects in scenes (Gronau et al., 2008; Henderson et al., 2007, 2008; Park et al., 2007), and EEG-guided fMRI evidence that category decision effects with visually impoverished cars and faces reflect interactions between right VLPFC (BA 47/12) and LOS (Philiastides & Sajda, 2007).

3.6 PHT Processes Modulate Knowledge

To explain how PHT modulates knowledge and meaning, MUSI capitalizes on the interactive activation and competition theory of object naming (Humphreys et al., 1999), which suggests how object and word knowledge interact. This theory posits several knowledge systems with recurrent internal connections within each. A ‘structural description’ system for the perceptual form of object categories is proposed at the entry level to semantics (e.g., dog, car, saw), which interacts reciprocally with a ‘semantic representation’ system about functional and associative knowledge. This interacts reciprocally with two other systems for ‘name representation’ and general ‘semantic classification’ (e.g., animal, vehicle, tool). MUSI hypothesizes the following. (a) To name an

object, visual object knowledge (e.g., structural descriptions) in the inferotemporal part of the PHT testing system activate during the frontopolar N3. Indeed, left posterior inferotemporal cortex is implicated in structural descriptions for naming (Humphreys et al., 1999) and shows categorization-specific view effects (Schendan & Stern, 2008). (b) Semantic representations of objects in the posterior parts (fusiform and LOS) of the PHT prediction system activate during the frontocentral N3. (c) Name representations activate during the centroparietal N400. Notably, these knowledge processes are affected by visual impoverishment during categorization (Schendan & Ganis, 2015; Schendan & Kutas, 2003; Schendan & Lucia, 2012; Schendan et al., submitted). Visual impoverishment affects the frontopolar N3 around 270 ms, the frontocentral N3 component around 310 ms and the centroparietal N400 around 390 ms (Schendan et al., submitted), suggesting a temporally overlapping sequence of influence on category decisions from visuospatial knowledge underlying the frontopolar N3, object knowledge underlying the frontocentral N3 and more abstract, multimodal and name-related knowledge underlying the N400. Consistent with this, magnetoencephalographic findings with pictures of real objects indicate that anterior temporal regions implicated as a source of the centroparietal N400 and fusiform regions implicated in model prediction during the frontocentral N3s show more phase locking, which reflects interactive and recurrent processing, with greater semantic integration demands between 200 and 500 ms (Andrews, Clarke, Pell, & Hartley, 2010). Altogether, this interactive activity may support automatic simulation to ground cognition, including constructing meaning (Barsalou, 2009; Ganis & Schendan, 2011).

3.7 Categorization, Similarity, Novelty and generalization

Most generally, the MUSI account attempts to explain the human brain's remarkable ability to generalize: To see and decide that novel visual configurations, such as a dog in fog, cloud formations, abstract paintings, or newly created objects (e.g., Segway, cell phone, iPod), are similar to known object structures. Future work should further test the more general hypothesis that PHT networks in state 2 are recruited depending upon the degree of similarity of the visual percept to stored object knowledge, which can vary not only with the degree of image impoverishment but also the statistical regularities of object features and/or their spatial configuration. Evidence for this has been reviewed above. Key additional evidence comes from "pseudo-object" effects, in which pictures of real objects are compared to pictures of pseudo-objects, such as objects with novel features, novel spatial configurations, and real objects combined into a novel figure, and people perform a variety of tasks, such as object or reality decisions, category or memory decisions, or passively view the pictures (e.g., Kroll & Potter, 1984). In ERP and fMRI studies, the N3 complex is more negative and the PHT networks are more active for pseudo-objects than real objects (Barbarotto, Laiacina, Macchi, & Capitani, 2002; Daffner, Mesulam, Scinto, Calvo, et al., 2000; Ganis et al., 2007; Gruber & Muller, 2005, 2006; Holcomb & McPherson, 1994; McPherson & Holcomb, 1999; Michelon, Snyder, Buckner, McAvoy, & Zacks, 2003; Schendan & Ganis, 2015; Schendan et al., 1998). Crucially, this is the same pattern as for impoverishment effects, that is, comparisons between more than less impoverished real objects. Together, similarity of impoverishment and pseudo-object effects suggests a more general role for top-down frontoparietal PHT functions. These processes determine that any visual structure that may be ambiguous (e.g., wallet vs. gun held by crime suspect) or novel, and thus visually dissimilar from stored knowledge (e.g., a truck through fog, abstract art, cloud formations, novel artifacts), nonetheless resembles a previously-experienced object.

Thus the MUSI account proposes that PHT processes, such as those in state 2, serve the more

general purpose of resolving perceptual discrepancies between perceived input and stored object knowledge, thereby supporting generalization. Such resolution could provide the “teaching” feedback signal to induce new learning about novel visual characteristics, consistent with ERP and fMRI evidence implicating these networks in category learning (Curran et al., 2002; Fazl et al., 2009; Jiang et al., 2007; Little & Thulborn, 2006; Reber, Gitelman, Parrish, & Mesulam, 2003; Scott et al., 2006), and evidence that attention processes, which are implicated in PHT (Ganis et al., 2007), can alter visual appearance (Carrasco, Ling, & Read, 2004). After all, image impoverishment is detrimental to performance because it alters how similar the percept is to stored knowledge (e.g., depth-rotation changes features and global spatial configuration, phase scrambling affects the spatial location of features). Consequently, the visual input is a poor fit to the statistical regularities of the object category. People can decide about the similarity to object knowledge and meaningfulness of novel visual shapes, even geometric shapes and random squiggles (Ganis et al., 2007; Voss & Paller, 2007; Voss et al., 2010). Most, if not all, images of an object deviate somehow from stored knowledge and memory, and these stored representations are imperfect, even when well-learned (Connor et al., 2007; Ganis et al., 2004; Gold, 2006; M. K. Johnson, 1997; Platt & Huettel, 2008). Perceptual similarity is a crucial part of a grounded cognition account of categorization (Goldstone, 1994). Most psychological theories of categorization incorporate the idea that an object is automatically determined to be a member of a category based on similarity, and the notion of similarity is constrained by the visual system and processes for integrating multiple sources of similarity information. Perceived shape similarity drives neural responses in monkey inferotemporal and human occipitotemporal cortex and is important for category learning (Cichy et al., 2019; Freedman et al., 2001, 2002, 2003; Jiang et al., 2007; Jozwik et al., 2016; Kriegeskorte, Mur, Ruff, et al., 2008; L. Li et al., 1993; Op de Beeck, Wagemans, et al., 2008; Rainer & Miller, 2000; Sigala, 2004; Sigala et al., 2002; Sigala & Logothetis, 2002).

3.8 Higher-Order Cognition and Task

The N3, and state 2 processes, in general, reflect processes that use perceptual information, initially computed in state 1, in the service of higher-order cognitive computations, such as decision-making and achieving task goals, as well as learning, memory encoding and retrieval, especially implicit memory and priming, novelty detection, attentional orienting, automatic mental simulation, and phenomenological consciousness. It is important to highlight that this means that state 2 processes support two general higher-order cognitive abilities: (a) activation of memory, especially knowledge and semantic memory, for higher-order cognition and/ or (b) modulation of higher-order cognition according to task goals (e.g., using cognitive control, attention, and response preparation abilities), but, nonetheless, such higher-order memory computations can happen automatically, regardless of task or decision-making or even without a task during passive viewing. For example, perceptual information can activate memory, especially knowledge and semantic memory, using recurrent and top-down feedback computations to enable higher-order representations (e.g., more global, feature-binding, integrated representations that may require attention as in feature-integration theory (Treisman, 2006)), regardless of task. MUSI theory suggests that recurrent and top-down feedback processes alter the function of a neuron or set of neurons in a cortical area such that they can perform computations that are not possible based on purely bottom-up (feedforward) information processing. Thus the recurrent and top-down feedback processes that are an essential, defining characteristic of state 2 enable a set of neural functions or computations that are not possible in state 1, regardless of task. However, modulation as a function of task or attention is an additional way that functions differ in state 2 compared to

state 1. Note, attention and task modulate processing also in state 1, but the function or the computations achieved as a result of this modulation differs from state 2. For example, the extreme case of top-down modulation used for strategic mental imagery affects both the N3 in state 2 and the VPP/N170 in state 1, albeit much less in state 1 than 2 (Ganis & Schendan, 2008; Schendan & Ganis, 2012). Also, the N3 pseudo-object effect occurs even when the image is task-irrelevant and a non-target stimulus, and the task on targets does not require categorization (e.g., detect red color, Schendan, 1998; Schendan et al., 1998), suggesting higher-order computation of object novelty (i.e., unknown pseudo-object) is a function of state 2, regardless of whether categorization is task relevant. It is also important to emphasize that state 2 involves many higher-order processes, and the N3 is a complex of components such that different components reflect different brain functions (e.g., varying with role in decision-making, memory, and task), and function may vary further with the context or task.. For example, the D220 component reflecting difficulty of two-choice decisions differs between easy and hard perceptual conditions (high vs. low phase coherence) when the task is face-versus-car discrimination, which may be done based on detecting a single feature (e.g., detect eyes), but not when the task is discriminating red-versus-green color (Philiastides et al., 2006). This task-dependence has been taken as evidence for a true top-down influence on decision-making, recruiting task-relevant attention and PHT processes, rather than merely bottom-up stimulus processing.

3.9 State 2 Timing

One striking feature of mid-latency negativities is that experimental manipulations generally affect amplitude and have little or no effect on latency, and there seem to be lower limits to the onset, consistent with the obligatory nature of neurophysiological states such that state 1 processing needs to reach a point that provides sufficient information for state 2 to begin to operate, and so on. Nonetheless, negativities related to decision making, such as the N2(00), which MUSI hypothesizes is an early component of the N3 complex in state 2 (Folstein & Van Petten, 2008; Schendan & Lucia, 2010), can vary in amplitude and latency with response time (Ritter et al., 1979). Further, depending upon the stimuli and task, the onset of N3 effects of category decision success can vary (a) from around 154 to 170 ms on 2-choice, ultra-rapid categorization tasks, which involve the fastest processing (Thorpe et al., 1996), (b) to between 175 and 218 ms for pseudo-object effects between intact real categorized objects and pseudo or degraded uncategorized objects on simple tasks (Gruber & Muller, 2006; Gruber et al., 2006; Holcomb & McPherson, 1994; McPherson & Holcomb, 1999; Sehatpour et al., 2006), (c) for impoverishment effects comparing levels of visually degraded drawings between 230 and 255 ms using a simple object detection task (Schendan & Ganis, 2015) (d) or between 232 and 364 ms on an open-ended naming task which involves the slowest processing (Doniger et al., 2000; Schendan & Maher, 2009), (e) with repetition priming, which reduces the onset by over 50 ms from 316 ms for new objects down to 252 ms for repeated objects (Schendan & Maher, 2009).

4 STATE M: Details and further evidence

State M operates after about 300 to 500 ms and lasts until about 900 ms or longer to perform internal evaluation and higher-order PHT or verification functions, which can be conscious and effortful. Evaluation functions evaluate internally the accuracy of earlier and ongoing decision and memory processes. Higher-order PHT or verification functions include effortful, strategic, conscious processes for cognitive control, working memory, executive function and mental simulation (i.e., conscious effortful processes involved in mental imagery or mental rotation). These processes have a greater role during more complex cognitive tasks. These brain dynamics

are reflected in P3b/P3(00)-like late ERPs. These late positive-going ERPs reflect a distinct kind of decision process that uses information from the earlier decision function (e.g., selected/retrieved categories or meanings) to classify stimuli into a task-relevant response type (e.g., Dien, Spencer, & Donchin, 2004; R. Johnson, Jr., 1984, 1986; Polich, 2007; Sutton & Ruchkin, 1984).

Categorization success modulates a P3(00)-like ERP, specifically, an occipitoparietal P600 between 500 and 700 ms, which seems related to internally evaluating the success of earlier (e.g., N3) decision processes in state 2 (Schendan & Kutas, 2002; Schendan & Maher, 2009) and potentially higher-order semantic processing beyond the N400. The P600 is more positive for better memory matches, more confident and successful categorization, and canonical than unusual views on categorization (Schendan & Kutas, 2003), and a semantic P600 has been reported for semantic anomalies in language research (Leckey & Federmeier, 2019), suggesting a semantic evaluation role (van Herten, Kolk, & Chwilla, 2005) perhaps related to the name of the object with picture stimuli.

In addition, on categorization or episodic recognition tasks, another late P3-like potential is modulated: the centroparietal late positive complex (LPC). The LPC is an exceptionally large, broadly distributed ERP reflecting large-scale frontoparietal network activity and so likely reflects multiple processes. Later verification of category decisions, complex semantic analysis, and episodic recognition have been associated with a posterior LPC between 500 and 900 ms (Schendan & Kutas, 2002; Sitnikova et al., 2008; Voss et al., 2010). The LPC reflects strategic top-down activation of memory, as factors of impoverishment, mental imagery, semantic context, and deception modulate the LPC and do so differently from the earlier N3, thereby dissociating states 2 and M (Ganis, Schendan, & Keenan, 2013; Schendan & Ganis, 2012; Schendan & Lucia, 2009; Schendan & Maher, 2009). For example, on category decision tasks, the LPC distinguishes between correct and wrong decisions but does not vary with how well the stimulus matches memory, which, by contrast, sensitively modulates the N3 (Schendan & Kutas, 2002; Schendan & Maher, 2009).

On episodic memory tasks, numerous studies have established the LPC as a marker of episodic memory retrieval, including recollection. On episodic recognition tasks, the parietal LPC between 500 and 900 ms is modulated with performance that suggests access to the episodic memory signal in the MTL, being typically more positive for old or familiar than new items, for information remembered better than less well from the study episode, and for high than low confident decisions, especially for old items (e.g., Curran, 2004; Wynn, Daselaar, Kessels, & Schutter, 2019; Yovel & Kanwisher, 2004). Notably, even within the MTL, episodic recollection, familiarity and novelty signals can be detected and dissociated (Daselaar, Fleck, & Cabeza, 2006), suggesting potentially complex interactions depending upon the stimuli, task, and experience. Some theories of recognition suggest that the strength of an episodic memory signal is evaluated for all stimuli, both old and new items. The LPC may reflect, at least in part, this evaluation process itself, not just the episodic memory signal. Consistent with this, the LPC shows a task effect even with unstudied objects that carry no (or minimal) experimental memory signal, being larger on episodic recognition than categorization (Schendan et al., submitted). This LPC modulation is smaller than the characteristic difference between old and new items and may reflect engagement of processes that evaluate the episodic memory signal, including attempts at recollection even when they fail and even with new items. The LPC varies with episodic recollection, as when recalling details of the learning experience during recognition and mental imagery tasks (Rugg & Curran, 2007; Schendan & Ganis, 2012). In general, many LPC modulations resemble those in a default mode network that connects strongly with the MTL system for episodic memory and is associated with

episodic simulation and strategic, conscious mental imagery (Ganis & Schendan, 2011; Schacter, Addis, & Buckner, 2008). Such late processes, however, may also support complex semantic analysis beyond the N400 (e.g., Sitnikova, Goff, & Kuperberg, 2009). Supporting this proposal, while 8-9 year old children show N300 and N400 congruency effects, they have not yet developed the LPC congruency effects seen in adults (Maguire et al., 2013). Thus the LPC reflects internal evaluation and PHT or verification processes that also support strategic, conscious, goal-driven, complex semantic processes, and strategic mental simulation that can contribute to grounding cognition in more abstract and complex ways than earlier automatic mental simulation. Finally, other late ERPs may also operate in state M or constitute a later state, such as a late frontal slow-wave after 700 ms that is observed on categorization and episodic recognition tasks that may reflect response related activity (Schendan & Ganis, 2015) or retrieval orientation (Schendan et al., submitted) or other late functions.

4.1 Object Constancy.

MUSI proposes that state M contributes top-down PHT feedback processes involving strategic contributions from cognitive control, working memory, and selective attention functions in frontoparietal cortex, especially if state 2 PHT processes fail or result in an uncertain decision. According to a hybrid MVPT-verification PHT theory, strategic mental imagery processes, such as mental rotation, contribute to spatial transformation for hypothesis testing after 500 ms. Consistent with this, impoverishment affects processing not only during state 2 but also after 500 ms during state M (Schendan & Ganis, 2015; Schendan et al., submitted).

4.2 Multiple-Network Interactive Dynamics.

A MUSI account suggests that, to make category and recognition decisions about visual objects, initial bottom-up activation of visual cortical pathways happens in State 1 supporting basic functions like categorical perception. Next, parts of the active task network operate during the N3 complex for higher cognitive functions, especially decision-making, constructing meaning from perceptual information, and automatic simulation for embodied cognition (State 2). Next, State M operates to internally evaluate the earlier decision and memory processes (from earlier states) and strategic mental simulation for embodied cognition during the P600, and any recollection and strategic episodic mental simulation during the LPC and late slow-wave. State M processes involve frontoparietal cortex, the default mode network and the MTL. Notably, these internal evaluations can occur even for new items to serve the task goal of making an appropriate response (e.g., indoor *vs.* outdoor; new *vs.* old). MUSI proposes that state 2 initially and predominantly reflects active task (or frontoparietal control) and other (e.g., salience or dorsal attention) network activity, whereas state M includes default mode network activity on explicit memory tasks, such as categorization and especially recognition. This is based on a large body of convergent evidence of similar patterns of effects during state 2 and active task regions versus state M and default mode regions. For example, similar patterns between these states and their respective networks have been seen across parallel ERP (Schendan & Ganis, 2015; Schendan & Kutas, 2003; Schendan & Lucia, 2009, 2010; Schendan et al., submitted) and fMRI studies of categorization, implicit memory, episodic memory, and mental imagery (Ganis et al., 2007; Schendan, submitted; Schendan & Lucia, 2012; Schendan & Stern, 2007, 2008).

However, the story is complex and must await future work to clarify. For example, the MUSI account suggests that state 2 is predominantly active task network activity, indexed by N3 complex and N400, and this is consistent with the associated neuroanatomy, but some studies suggest N400 and semantic memory for words at least in part reflects contributions from the default mode network. Semantic memory involved in language comprehension includes modality-specific and

supramodal (polymodal, multimodal) cortex, including inferior parietal and most of temporal cortex that are parts of the default mode network and convergence zones for multiple perceptual processing pathways (Binder & Desai, 2011; Binder, Desai, Graves, & Conant, 2009). Semantic memory and object processing has been proposed, controversially, to extend from occipitotemporal cortex into parahippocampal and even hippocampal regions along a pathway in which semantic memory processes become increasingly abstract and complex and increasingly contribute to episodic memory (e.g., A. C. Lee et al., 2006; C. B. Martin et al., 2016; Quiroga, Kreiman, Koch, & Fried, 2008). Notably, an N400-P600 complex is often observed during higher cognitive tasks, suggesting a close, perhaps interactive yet dissociable relationship between the underlying neural processes. The MUSI account suggests there may be a transition between high-level, more abstract semantic memory and episodic memory during the N4-P6 complex.

The MUSI account hypothesizes that the transitions between states are generally dynamic, interactive and complex. Such complexity is illustrated, for example, by the interactive dynamics increasingly understood about the active task networks that predominantly contribute to state 2 and the default mode network regions, including the MTL, that predominantly contribute to state M. The default mode network has a role not only in internal evaluation but also more broadly for externally-directed higher cognition involving a memory-related function (Vatansever, Manktelow, Sahakian, Menon, & Stamatakis, 2018). The particular combination of network dynamics likely depends upon the stimulus and task processing demands and how these affect allocation of attention. For example, parts of the default mode network may switch attention to the active task network (Corbetta & Shulman, 2002), and the active task (or frontoparietal control) network is highly interconnected with the default and other networks and mediates internetwork interactions (Spreng et al., 2013).

Consequently, MUSI hypothesizes further that state M reflects interactive dynamics among multiple functional networks, that is, frontoparietal control, salience, and default mode, with the latter having a particularly strong role as a regulator of network dynamics especially when the task or situation recruits episodic memory processes, strategic mental simulation, or internal evaluation of response planning, decisions or memory. For example, divergent thinking processes have a central role in creativity and are associated primarily with default mode network activity, which also interacts dynamically with frontoparietal control (and salience) networks for creative cognition (Zhu et al., 2017). However, given the anti-correlated nature of these networks, each may contribute in state M at different periods of time, and state M likely reflects multiple states, itself (e.g., default mode vs. frontoparietal control state), which is a question for future work.

Further evidence for closely related and interacting yet dissociable processes around the transition between states 2 and 3 focuses on the MTL. This includes evidence that the MTL is independent yet can also be strongly associated with the default mode network during episodic memory tasks (Buckner, Andrews-Hanna, & Schacter, 2008). Moreover, ERP studies of people with MTL dysfunction indicate that MTL-related activity supports episodic memory function during the LPC and P600, while default mode network activity also contributes to semantic memory function during the P300 and N400. Consider that the MTL supports episodic memory, and circumscribed MTL lesions produce amnesia (i.e., episodic memory problems) and alter the plasticity of the LPC, including the P600 (J. R. Taylor & Olichney, 2007). In contrast, Alzheimer's dementia affects both the MTL and neocortical association areas of the default mode network, resulting in both episodic and semantic memory problems, and abnormal P300, N400, and P600 (Olichney et al., 2006; Olichney et al., 2013). The MUSI account hypothesizes that the N400 reflects a transformation from modal knowledge and semantic processing during the N3 complex

in state 2 into supramodal (polymodal, multimodal) higher-level, more abstract semantic processing and word-related knowledge during the N400 in state 2, with the underlying neural generators also contributing to using knowledge and semantic memory to support higher-order semantic analysis during categorization tasks or episodic memory processes in the MTL during episodic memory tasks in state M.

5 FUTURE DIRECTIONS, CONCLUSIONS & OVERALL TIME COURSE

Overall, convergent evidence, especially from ERP studies, supports the MUSI account of the cortical dynamics unfolding over time to support visual object cognition, memory and knowledge (Figures 1-2). The MUSI account proposes, in the first state, initial, bottom-up activation of object-sensitive occipitotemporal cortex occurs between around 95 to 115 ms to around 150 to 250 ms. State 1 can support several functions: detecting salient shapes against a background (object-sensitivity, between 95-115 and 180 ms, and again after 200 ms), categorical perception (between 120 and 170-200 ms), perceptual grouping (between 150 and 250 ms), and perceptual implicit learning and memory for these processes. However, state 1 cannot support higher cognition or decisions which happen later. Starting between ~150-230 ms and lasting until around 500 ms or later, with time course varying with stimulus and task conditions, in state 2, there is sustained interactive activation of object processing areas, especially in object-sensitive occipitotemporal cortex, that involves top-down, recurrent, and bottom-up processes among these areas and with occipitoparietal and prefrontal cortex. During tasks in which there are little or no expectations (e.g., the response is open-ended or unknown, the stimulus is not pre-cued, no target is specified), State 2 is the first time when lateral prefrontal cortex modulates posterior processing according to the current behavioral context and goal in order to accomplish higher order cognitive functions (e.g., decision-making). This interactive activation provides the earliest, substantial and necessary computations that support decision-making, phenomenological awareness, knowledge retrieval and implicit memory. For example, for a category decision, state 2 supports object model selection: selecting the best match to the percept from among stored object models to make a decision. Further, following initial categorical perception of objects in state 1, interactive, top-down and reflexive feedback, and recurrent processes in state 2 support automatic mental simulation to ground knowledge and meaning (Barsalou, 2009) in modal processing of visual features in occipitotemporal cortex (N3) and multimodal and/ or word-related semantic processes in anterior temporal cortex (N400). Also in state 2, top-down processes of PHT in prefrontal and occipitoparietal cortex can modulate occipitotemporal cortex to enable model selection even with highly impoverished visual images, thereby achieving the visual constancy of object cognition. PHT involves iterative cycles of activity in a brain system for hypothesis prediction and another system for hypothesis testing. PHT processes serve the more general purpose of resolving perceptual discrepancies between perceived input and stored object knowledge and memory: Generalization. The MUSI account hypothesizes that PHT processes in state 2 support object constancy, thereby enabling the remarkable ability to resolve perceptual ambiguity and novelty in the real world -- that is, to see and decide that novel visual shapes resemble known object structures. Such abilities can also enable surrealist or abstract art (e.g., 'Bird in Space' by Brancusi, 1932-1940) to be interpreted as meaningful. State M operates from about 300 to 500 until 900 ms or longer during P3(00)-like ERPs when internal evaluation and higher-order PHT or verification functions operate, which can be conscious and effortful. These operations can involve a default mode network especially for memory-related functions, which also interacts with other large-scale cortical networks (e.g., frontoparietal, salience). State M supports the second type of mental

simulation, which is strategic, goal-directed, and conscious and recruited when the task demands internal evaluation of cognition, as in mental imagery and episodic memory tasks. This strategic mental simulation reflects intentional top-down processes involving multiple cortical networks, including lateral prefrontal and posterior parietal networks for attention, cognitive control, and working memory.

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